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THE UNIVERSITY OF ALBERTA

Ecology of a population of stunted yellow perch (*Perca flavescens* Mitchill)

by

Toni-Lynne Jacobson

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Date..Oct 12 1989

ABSTRACT

This study examined characteristics of stunted yellow perch (*Perca flavescens* Mitchell) in a small Boreal Forest lake to evaluate their contribution to slow growth. I hypothesized that perch were competing for limited food resources and that this competition resulted in stunting. The hypothesis was tested by determining the effects of fish density on the growth and diet within the dominant size class of perch using enclosures located in the littoral zone. Growth in weight was used as a measure of competition. Changes in diet and the invertebrate community were used as indicators of how growth was limited.

The perch were the slowest growing perch yet reported in Canada. The population was dominated (>80% by biomass) by perch <80 mm total length (TL) of which 80% were age 1+. High population density (3100±1200 perch/ha), high mortality rate, small size (<70 mm TL) and age (1+) at maturity (males), and the extremely slow growth rate result in a population dominated by young, small-bodied individuals. Growth rate of age 1+ perch decreased during July and condition decreased from May to August. The decreases corresponded to a time of decreased macroinvertebrate biomass and zooplankton density in the littoral zone. Stomach fullness (mg food/g fish) of perch (2.51-4.00 g), which ate predominantly amphipods until August, decreased in July, as did amphipod biomass in the littoral zone. Macroinvertebrates were more important in the diets in early summer and microinvertebrates more important in late summer of perch <4.0 g and <85 mm TL.

Growth and condition were inversely related to perch density within enclosures, providing evidence of intraspecific competition. The effect was more pronounced in August than earlier in the summer: perch at high density lost weight in August whereas they gained weight when held at the same density in July. More microinvertebrates were eaten in August than July. Stomach fullness and the proportion of microinvertebrates eaten were inversely related to density at densities $\geq$6.8 g/m^2. Increasing levels of competition led to inclusion of more microinvertebrates and rare prey items in the diets of perch. Biomass of amphipods decreased significantly at perch densities equal to and greater than 6.8 g/m^2. When abundance of preferred prey decreased, perch ate prey taxa not previously included in their diets. Perch

held at a density of 3 g/m² in July grew significantly faster than perch in the lake (2.6 g/m²), suggesting that all age classes were competing for limited amounts of invertebrates in the lake.

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Table of Contents

Chapter — Page

I. GENERAL INTRODUCTION 1

A. COMPETITION 2

Density dependent growth 3

Limited food resources 4

B. HYPOTHESIS 5

LITERATURE CITED 7

II. CHARACTERISTICS OF A POPULATION OF STUNTED YELLOW PERCH IN A BOREAL FOREST LAKE 10

A. INTRODUCTION 10

Purpose of population study 12

B. MATERIALS AND METHODS 12

Study lake 12

Sampling 13

Population size and biomass 16

Growth dynamics 16

C. RESULTS 19

Population size and biomass 19

Population structure 19

Mortality 25

Growth dynamics 25

Sexual differences in growth of age 1+ perch 29

Length-weight relationships 29

D. DISCUSSION 34

Growth 34

Condition 39

Population structure 40

Mortality 44

Reproduction 45

LITERATURE CITED 47

III. EXPERIMENTAL EVIDENCE FOR COMPETITION IN A STUNTED PERCH POPULATION 51

A. INTRODUCTION 51

B. METHODS AND MATERIALS 52

Enclosure construction and location 52

1986 Experimental protocol 53

1987 Experimental protocol 55

Stocking and recovery of perch in the enclosures 55

C. RESULTS 57

1986 Experiments 57

1987 Experiments 62

D. DISCUSSION 68

LITERATURE CITED 70

IV. EFFECT OF COMPETITION ON THE DIET OF STUNTED YELLOW PERCH ..72

A. INTRODUCTION 72

B. METHODS AND MATERIALS 76

Enclosure experiments 76

Sampling protocol for 24-h feeding study 77

Procedure for examining stomach contents 78

Analyses of stomach contents for competition experiments 78

Analyses of stomach contents of perch from the lake 80

Invertebrate collection 80

C. RESULTS 81

Twenty-four hour feeding study 81

Stomach contents of perch from the lake 84

Invertebrate prey availability 88
1986 Experiments 93
1987 Experiments 102
D. DISCUSSION 111
Intraspecific competition 111
Diet of perch in Narrow Lake 113
LITERATURE CITED 118
V. GENERAL CONCLUSION 121
LITERATURE CITED 124
APPENDIX 1. Supplementary Tables for Chapter 2 125
APPENDIX 2. Supplementary Tables for Chapter 3 130
APPENDIX 3. Supplementary Tables for Chapter 4 132

List of Tables

Table		Page
2.1	Biomass and density of the fish population in Narrow Lake, 1986-1988	20
2.2	Biomass distribution and proportion of biomass in weight size categories of perch in Narrow Lake in 1986-1988	24
2.3	Comparison of the average size of age 1+ male and female perch from Narrow Lake in August 1986-1988.	32
2.4	Size at age of stunted perch in various lakes.	37
2.5	Size and biomass of populations of stunted and non-stunted perch in various lakes.	41
3.1	Recovery schedule of perch in two enclosure experiments conducted in 1986 testing for evidence of intraspecific competition	59
3.2	Recovery schedule of perch in three enclosure experiments in 1987 testing for evidence of intraspecific competition.	63

3.3 Number of perch gaining and losing weight when stocked at various densities in enclosures in three experiments in 1987 testing for evidence of intraspecific competition.....65

4.1 Stomach contents (% by weight and frequency of occurrence) of two size classes of perch in Narrow Lake during June-August, 1986 85

4.2 Stomach contents (% by weight and frequency of occurrence) of three size classes of perch in Narrow Lake during May-August, 1987.....87

4.3 Stomach contents (% by weight and frequency of occurrence) of perch in enclosures at low and high perch densities in experiments testing for intraspecific competition in 1986. 96

4.4 Benthic invertebrate community in enclosures at low and high perch densities in two experiments conducted in 1986 testing for intraspecific competition. 100

4.5 Stomach contents (% by weight and frequency of occurrence) of perch in enclosures at various densities in experiments testing for intraspecific competition in 1987. 104-105

4.6 Benthic invertebrate community in enclosures at various perch densities in the experiment conducted in June, 1987, testing for intraspecific competition. 109-110

List of Figures

Figure		Page
2.1	Sampling sites for perch at Narrow Lake, Alberta	15
2.2	Length frequency distributions of perch caught by block seine in Narrow Lake, Alberta	21
2.3	Biomass distribution of perch caught by block seine in Narrow Lake, Alberta	22
2.4	Growth in weight of age 1+ perch in Narrow Lake during May-August, 1986-1988.	26
2.5	Growth in length of age 1+ perch in Narrow Lake during May-August 1986-1988.	27
2.6	Relation between growth increment of age 1+ perch and average water temperature in the littoral zone of Narrow Lake during 1986-1988.	30
2.7	Average water temperature in the littoral zone (surface to 6 m depth) of Narrow Lake during 1986-1988	31
2.8	Length-weight relationships of age 1+ perch during 1986-1988.	33
2.9	Change in condition (K) of age 1+ perch during May-August, 1986-1988.	35

2.10 Back-calculated total length at age of yellow perch in various Alberta Lakes. 36

3.1 Sampling sites and site of enclosure experiments in Narrow Lake, Alberta 54

3.2 Average growth of perch in enclosures at low and high perch densities in two experiments in 1986 testing for intraspecific competition 60

3.3 Condition (K) of perch in enclosures at low and high perch densities in two experiments in 1986 testing for intraspecific competition. 61

3.4 Average growth of perch in enclosures at various perch densities in three experiments in 1987 testing for intraspecific competition 64

3.5 Condition (K) of perch in enclosures at various perch densities in three experiments in 1987 testing for intraspecific competition. 67

4.1 Stomach fullness (mg food/g fish) and % of perch with empty stomachs for perch (<85 mm TL) in Narrow Lake during 24-h sampling on July 8-9, 1986. 82

4.2 Stomach fullness (mg food/g fish) and % of perch with empty stomachs for perch (<85 mm TL) in Narrow Lake during 24-h sampling on August 3-4, 1986. 83

4.3 Summer % composition (by weight) of the diet of two size classes of perch during 1986 in Narrow Lake. 86

4.4 Summer % compostition (by weight) of the diet of two size classes of perch during 1987 in Narrow Lake. 89

4.5
Stomach fullness (mg food/g fish) of two size classes of perch during May-August, 1986 in Narrow Lake. 90

4.6
Average total benthic invertebrate biomass at the 1 m depth during the summer of 1986 in Narrow Lake. 91

4.7
Change in biomass of major benthic invertebrates at the 1 m depth during the summer of 1986 in Narrow Lake 92

4.8
Amphipods as a % by weight [(mg amphipods/mg total stomach contents)*100] in the diets of small (1.20-2.50 g) and large (2.51-4.00 g) perch and as a % of total benthic biomass at the 1 m depth in Narrow Lake during May-August, 1986. 94

4.9
Stomach contents (% by weight) of perch in enclosures at low and high perch densities and in the lake in 1986. 95

4.10
Proportion of microinvertebrates [(mg microinvertebrates/mg total stomach contents)*100] in the diets of perch in enclosures at low and high perch densities in 1986 97

4.11
Stomach fullness (mg food/g fish) of perch in enclosures at low and high densities in 1986 to test the effect of perch density on diet 99

4.12
Average biomass of macroinvertebrates in enclosures at low and high perch densities in 1986. 101

4.13
Stomach contents (% by weight) of perch in enclosures at various perch densities in 1987. 103

4.14
Stomach fullness (mg food/g fish) of perch in enclosures at various perch densities in 1987 testing the effect of perch density on diet 106

4.15
Proportion of microinvertebrates [(mg microinvertebrates/mg total stomach contents)*100] in the diets of perch in enclosures at various perch densities in 1987..... 107

4.16
Zooplankton abundance (No./L) in the littoral zone of Narrow Lake during June-August, 1986. 115

I. GENERAL INTRODUCTION

Many fish populations exist in which the majority of individuals are small-sized compared to fish of the same species in nearby waters that are of a more "normal" size for the species. In current usage, populations consisting almost exclusively of small bodied fish are termed stunted populations, and the small-sized individuals are called stunted. The term stunted always refers to the individuals in the population, not the population itself (Hackney 1979).

Stunted populations can be composed of fish having various growth patterns. Some stunted populations have normal or rapidly growing fish with a high mortality rate such that few individuals live long enough to grow to a normal adult size (Alm 1946, Hackney 1979). so the population is dominated by small individuals. In other stunted populations, the fish grow normally for the first few years of life then stop growing and remain small throughout the rest of their life. Other stunted populations can be composed of slowly growing fish which never reach a normal size regardless of life span. Stunted growth, or stunting, refers to the condition in which individual growth rates are well below the potential expected for the species (Burrough and Kennedy 1979) including the reduced growth of juveniles and adults or growth cessation of adults (Diana 1987).

Fish with stunted growth retain the potential for normal growth under different environmental conditions. When stunted lake trout, *Salvelinus namaycush* (Martin 1966), channel catfish, *Ictalurus punctatus* (Tiemeier and Elder 1960), brook trout, *S. fontinalis* (Reimers 1979), and yellow perch, *Perca flavescens* (Heath and Roff 1987) were transferred to different waters, the fish increased their growth rates and achieved a larger maximum size. Perch in Lake Windemere, considered stunted before 1941, increased growth rate over several years following an increase in harvest and were growing to a larger size by 1952 (Le Cren 1958). Thus, where it has been examined, the characteristic of stunting is not genetically fixed within a population. Instead, growth appears to be primarily controlled by environmental conditions.

Many factors can influence the growth and maximum size of fish. Some factors shown to reduce growth of fish under experimental conditions include changing photoperiod (Gross *et al.* 1965, Huh *et al.* 1976), temperature (Niimi and Beamish 1974), low oxygen (Adelman and Smith 1970), high salinity (Brett 1979) and high fish density (Allen 1974, Elliot 1982). However, under natural conditions in many lakes the evidence is inconclusive as to the cause or causes of stunting. Most often, stunted growth under natural conditions has been related to competition for space and food (Weatherley 1972). A common condition in which stunting is observed is monocultures of self-sustaining fish species in ponds and small lakes, where fish abundance increases rapidly and growth of individuals stops or is extremely slow (Hackney 1979). Stunting is hypothesized to occur in this circumstance because the fish are competing for limited food (Hackney 1979), which leads to reduced growth.

A. COMPETITION

Competition exists when different individuals seek a common resource or resources whose supply is insufficient for all or when individuals interfere with each other in obtaining that resource (Sale 1979). Competition has a deleterious effect on the competing individuals, since they obtain reduced amounts of the resource (Weatherley 1972). The effects of competition can be expressed as lowered fitness levels of the competing individuals by reducing growth rates, condition, survival, or fecundity (Sale 1979, Connell 1983). Stunting has been attributed to resource limitation as a result of competition (eg. Persson 1983a, b, 1986, Hackney 1979).

Moermond (1979) defines a resource as limiting if the use of that resource by an individual is negatively affected by another individual. Depending on the type of resource, competition can be classified into three categories that are applicable to fish: territorial, encounter, and consumptive competition (Schoener 1983). The first type, territorial competition, occurs if an individual aggressively defends or signals its intentions to defend a unit of space. The limiting resource is space, either for breeding or feeding purposes. Territorial competition would negatively affect reproduction and feeding of individuals which

do not have territories or have inferior territories. Thus, individuals with territories could be more fit than others without territories.

The second category of competition, encounter competition, results from interactions between competing individuals that cause harm, such as loss of time or energy, theft of food or bodily injury. The joint use of any resource could result in adverse affects for the users, even if the resources are not at some finite limit or are easily accessible (Moermond 1979).

Consumptive competition occurs when some quantity of a food resource is consumed by an individual therefore depriving others. The major consequence of less food available per fish is the reduced growth rate of individuals (Weatherley 1972). Death of the less successful competitors is unlikely because fish are flexible in their growth and can have negative growth rates for extended periods depending on the amount of energy available for body maintenance and growth (Weatherley 1972). However, consumptive competition also affects size related parameters such as fecundity and condition of individuals. When too many individuals who do not differ in foraging ability are competing for the available food resources, all of those individuals can be affected negatively.

Consumptive competition is the type of competition most often suggested as a cause of stunting. For example, if a fish population increases in size and there is no corresponding increase in food supply, the amount of food per individual is reduced and less energy will be available for growth (Backiel and Le Cren 1978). Evidence for competition and food limitation in natural populations of stunted perch is limited mainly to studies which indirectly show density dependent growth and food limitation.

Density dependent growth

An inverse relationship between population density and individual growth has been observed in many fish populations and is used as indirect evidence for competition. For example, the growth of stunted perch was found to be inversely related to perch abundance in several studies (Alm 1946, Eschmeyer 1937, Hansson 1985). Over a 30-year period, the year class strength and the number of pike and perch in Lake Windemere have decreased while

growth rates have increased (Kipling 1984). The onset and alleviation of stunting in roach, *Rutilus rutilus*, correlated with an increase then decrease in roach population density (Burrough and Kennedy 1979, Linfield 1980). Both mechanical and natural reductions in the population sizes of stunted rock bass, *Ambloplites rupestris*, (Beckman 1941, 1948), chain pickerel, *Esox niger*, largemouth bass, *Micropterus salmoides* (Grice 1959, Parker 1958), perch and roach (Persson 1986) were followed by increased growth of the remaining fish. Furthermore, the increases in growth rates of these stunted fish following population reductions were not maintained in those populations that subsequently increased in number. These studies suggest that high fish density operates indirectly through food shortages to limit growth (Murnyak *et al.* 1984). The intensity of competition for limited food resources, and therefore the effects of competition, depends upon the amount of food available per individual.

Few studies provide direct evidence that fish density is inversely related to fish growth. Hanson and Leggett (1985) manipulated the densities of non-stunted perch and pumpkinseed in enclosures in the littoral zone of a bay in Lake Memphremagog, Quebec, and found that growth of the fish was inversely related to stocking density. Persson (1987) used enclosures stocked with young-of-the-year perch and adult roach in a lake in Sweden to test if the fish were food limited and found that the growth of the young was negatively related to fish density. The conclusion from these studies is that competition for limited food resources will cause slower growth.

Limited food resources

A few whole lake studies indicate that populations of stunted fish are food limited. Eschmeyer (1937) observed that the stunted yellow perch in small pothole lakes in Michigan were "starving". He concluded that inadequate food supply was responsible for the slow growth and poor condition of the perch. Tiemeier and Elder (1960) found that providing supplemental food to a population of stunted channel catfish stimulated faster growth. Under natural conditions, the amount of food available to the catfish was adequate for maintaining

a dense population of small-bodied fish but was insufficient for good growth of the fish. High density of perch in a small forest lake in Finland was thought to reduce the abundance of benthic fauna (based on analyses of stomach contents) and cause stunting (Rask 1983). Stunting of salmonids has also been attributed to high fish densities and inadequate food supply (Reimers 1979, Donald *et al.* 1980).

B. HYPOTHESIS

Stunted perch are common in many lakes with dense populations that are self-sustaining and long-term. Although yellow perch is an important game fish, populations of stunted perch are frequently ignored by anglers and considered as nuisances. Most studies on stunted perch propose theories that overcrowding and limited food supply are the causes of stunting (Grimaldi and Leduc 1973, Rask 1983, Hansson 1985, Grice 1959) but do not test those theories directly. Furthermore, most studies promoting the premise that food limitation causes stunting do not simultaneously examine the availability of prey items in the lakes to test whether demand for food resources actually exceeds the supply (Werner 1986). For competition to occur, there must be a limiting resource. A few recent studies have provided evidence that food limitation affects growth rates (Mittelbach 1988, Osenberg *et al.* 1988) or have directly examined the mechanisms of density dependent growth (Hanson and Leggett 1985, Persson 1987), but no such studies have been done on stunted populations of yellow perch.

Stunted perch populations have rarely been investigated in Canada except for a study describing the growth of stunted perch in two Quebec lakes (Grimaldi and Leduc 1977), and another describing growth in two Alberta lakes (Norris 1984). In three of these populations, the perch were stunted as the result of slow growth. In Clear Lake, Alberta (Norris 1984), the stunted perch had normal growth but short life span and hence did not live long enough to grow to normal size. These studies did not investigate any other population characteristics or determine the cause of the stunting in the populations where the fish were slow growing.

The purpose of this research was to investigate the population characteristics of stunted yellow perch in an oligomesotrophic Boreal Forest lake in western Canada and to determine the causes of stunting of these perch. I tested the hypothesis that competition for a limited amount of invertebrate prey results in the stunting of the perch by using controlled field experiments with enclosures located in the littoral zone and stocked with various densities of perch.

This thesis is divided into three parts. Chapter 2 describes the population characteristics of the stunted perch, including population size and biomass, population structure, and growth and mortality of age 1+ perch. Chapter 3 presents the field experiment testing directly for evidence of competition using growth as the measure of fitness. Chapter 4 discusses the temporal and size-related variability in the diets of juvenile perch and examines the effects of competition on the diet of perch stocked in the experimental enclosures.

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II. CHARACTERISTICS OF A POPULATION OF STUNTED YELLOW PERCH IN A BOREAL FOREST LAKE

A. INTRODUCTION

Many studies dealing with stunted fish examine only growth and disregard other population characteristics in favor of relating growth of the stunted fish exclusively to environmental factors such as temperature, food, and predation. However, growth rate will be determined in part by the amount of food available per individual, which will be dependent on size and structure of the fish population and that of their prey. In stunted populations there are few size classes of fish (eg. Sumari 1971, Rask 1983, Rask and Arvola 1985) because the majority of fish are small whether the fish are stunted as a result of slow growth, growth cessation at a small size or a high mortality rate. The number of individuals in each size class and the number of size classes in the population, i.e. the size structure, will influence the growth of the fish (Persson 1983). In turn, the size and structure of a population will be determined by the growth and mortality rates of the fish, as well as by other characteristics such as reproduction. Therefore, knowledge of all population characteristics is necessary for describing stunted populations and hence deducing the reasons for stunting.

Most fish populations are size-structured, i.e. they contain individuals of various sizes and body size determines such ecological characteristics as foraging ability, resource selection, fecundity, vulnerability to predation, and competitive interactions (Gilliam 1980). Resource use by fish is determined on the basis of characteristics such size of the individual fish. Thus within any size class of fish, resource use by all individuals is similar. When the resources used by any or all size classes of fish are insufficient to meet the demands of the population, competition will result. The intensity of competition will be related to total population size and the structure of the size classes.

Competition can occur both within a size class and among size classes of fish. However, within any species, small fish often use habitat and food resources distinct from those used by larger fish. Therefore, the potential for intraspecific competition within a size

class always exists, but competition may not occur between size classes or may be less intense. For example, the abundance of fingerlings, yearlings, and other fish species did not influence the total season's growth of first year bass (Kramer and Smith 1960), indicating a lack of competition between size classes. Schneider (1973) found the presence of high and low densities of fingerling perch did not affect the density-growth relationship of young-of-the-year perch. Growth of perch in single-species lakes was density-dependent within three size groups of perch (<8 cm, 8-16 cm, >16 cm), but density independent between size groups (Schneider 1973). Growth of perch and alewife in South Bay, Lake Huron, was affected more by year class strength than any other environmental factor, and Henderson (1985) and Henderson and Brown (1985) suggested that competition for food was most intense between similar sized individuals. In Lake Sövdeborg, Sweden, where perch were slow growing, diet overlap between size classes was high, and food consumption was low (Persson 1983). Persson (1983) concluded that all size classes of perch were competing for a limited amount of food. The number of fish within a size class appears to be more important in determining the effects and intensity of competition than the total number or biomass of all fish in the population (Henderson and Brown 1985).

Perch show size related ontogenic shifts in diets, passing through feeding stages in which they consume zooplankton, macroinvertebrates, and then fish as they grow larger (Clady 1974). Macroinvertebrates, such as dragonfly and mayfly nymphs, have a relatively long generation time, are more vulnerable to elimination by a predator than are zooplankton, and are therefore often in short supply (Keast 1977). When perch are slow growing so that several age classes are of similar size and a high density of fish occupy the size class which feeds on insects, a competitive bottleneck may exist (Gilliam 1980, Persson 1986). The bottleneck can restrict individual growth so perch do not progress to the next size class, which could use a broader range of resources such as fish for prey. The reduced growth results in a closer packing of size classes and a decrease in size class diversity (Persson 1983), and further contributes to reducing growth. Competitive bottlenecks also influences population size structure (Laughlin and Werner 1980).

Purpose of population study

The growth of fish and their demand for food cannot be determined by estimating the population size and food availability alone (Weatherley 1972). Other population characteristics are important in determining growth. The purpose of the present population study was to examine in detail the population characteristics of a stunted yellow perch population, in particular the population size, length structure and biomass structure of the perch in the littoral zone of a small Boreal Forest lake in central Alberta. A block seine was used to sample the whole size range of perch in the population to avoid weaknesses of other population studies which used traps and selected for fish greater than 85 mm. Gear selectivity may suggest a population structure lacking one or more age-size classes. I examined growth during the summer growing season of the age 1+ cohort. Few studies have followed the time course of growth during the growing season. Those that have suggest growth of young perch is constant throughout the summer months (Nyberg 1979) following slow growth in early spring.

B. MATERIALS AND METHODS

Study lake

Narrow Lake is a small (1.14 km^2), deep (mean and maximum depths 14.2 m and 36 m), oligo-mesotrophic lake in the southern boreal forest of central Alberta (54°35'N; 113°37'W). Summer chlorophyll *a* was 2.7 mg/m^3 and total summer phophorus was 10.4 mg/m^3 in 1986 (E. E. Prepas unpubl. data). Water chemistry and morphometry of the lake are described by Prepas and Trew (1983). The lower limit of the littoral zone in Narrow Lake was 6 m, the depth of the deepest rooted macrophytes. The littoral zone comprises 20.5% (23.4 ha) of the lake surface area (Hanson *et al.* 1988).

Water temperature data for the summers of 1986, 1987, and 1988 were obtained from E.E. Prepas, Department of Zoology, University of Alberta. Temperature was measured within 0.1°C at 14-day intervals at the surface and at 1-m intervals with a Montedoro

Whitney thermistor calibrated before each use. Average littoral zone temperature was calculated as the average temperature from the surface to 6 m for each sampling date.

Sampling

Fish were quantitatively sampled to estimate total fish biomass of all species, perch population size and the size structure of perch population in Narrow Lake between August 25 and 27, 1986; on June 2 and 5, 1987; August 24 and 26, 1987; and August 23, 1988. All fish were collected with a 60 m X 3 m sinking block seine with 5 mm (stretched) knotless nylon mesh. The seine was set by boat to enclose a 500-m^2 area from the shore to a depth of 4-5 m (depending on sampling site).

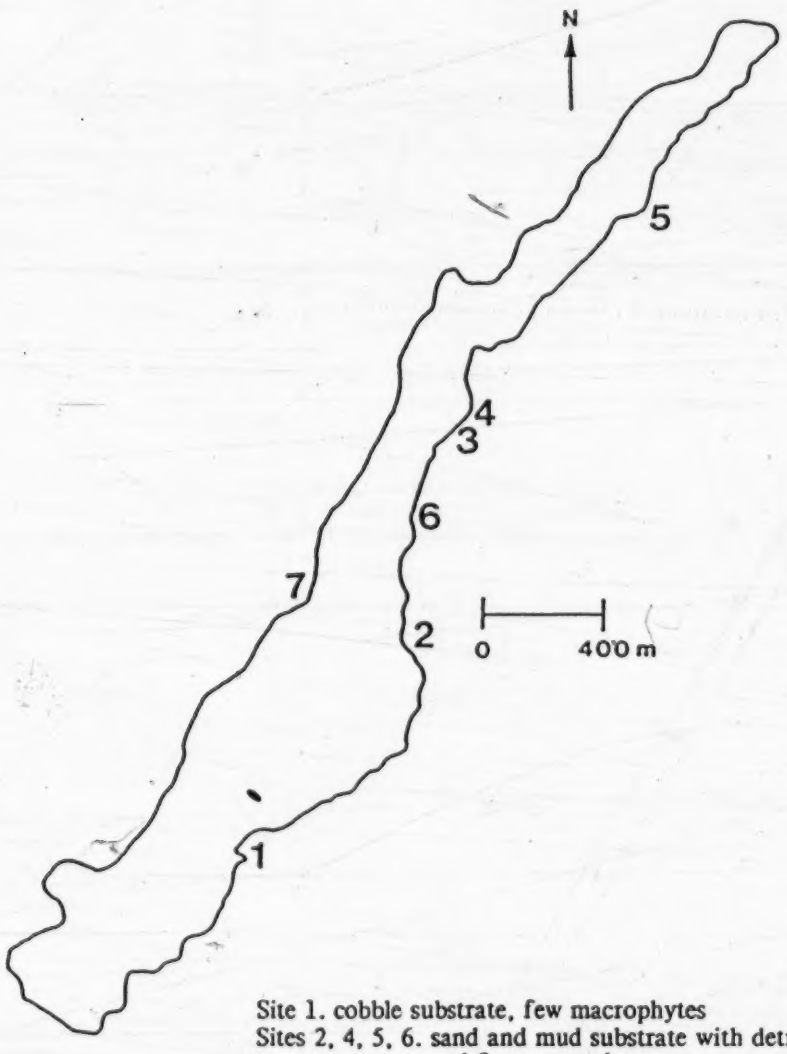
Similar sized seines have been assessed for capture efficiency by using mark-recapture (Boisclair and Leggett 1985) and by diver observation (Hanson and Leggett 1985). For each study, the efficiency was reported to be 100% for fish greater than 60 and 30 mm total length, respectively. Capture efficiency of the seine used in this study was assumed to be 100% for perch longer than 40 mm total length (TL, total length from anterior tip of snout to end of caudal fin). Some young-of-the-year (y-o-y) perch (average 38.7 mm TL August 19, 1986) were observed to escape through the seine mesh in August.

Block seining in the littoral zone has proven useful for estimating fish population size (Boisclair and Leggett 1985, Hanson and Leggett 1985). Perch commonly occur in the littoral zone of lakes throughout the spring and summer months (Thorpe 1977). Perch in Narrow Lake could easily be observed feeding in shallow water throughout the summer. However, large variation in number of fish caught and species composition can occur between sets and between collection sites (Bagenal 1972). Behavior of the perch will affect seining efficiency. Regular daily movements into and out of the littoral zone at sunrise and sunset are typical of yellow perch (Thorpe 1977). In some lakes during the summer perch occur close to shore on hot days (Lindström and Bergstrand 1979) and concentrate at lake margins at depths to 2.5 m (Keast and Harker 1977). Therefore, the efficiency of the block seine was examined for variation in catch between sampling times and between sampling sites in 1986.

Perch catch was dependent on the time of sampling. More perch were caught in the late morning and throughout the afternoon than were caught at other times (Appendix 1 Table 1). Therefore, only seine hauls done between 11:00 and 17:00 were used to estimate the population density and biomass since the perch appeared to use the littoral zone most frequently during this time of day. In 1987 and 1988, all sampling was done between 10:00 and 17:00.

Four sampling sites (1-4) on the eastern shore of Narrow Lake were used to collect perch for the population estimate in 1986 (Figure 2.1). Perch appeared to use all bottom types sampled equally except site 1 which was steep sloped with cobble substrate and was exposed to the prevailing wind. This site was abandoned after two seine hauls because of low catch, and it was excluded from the biomass estimates. Since sites 3 and 4 were within 50 m of each other they were combined for analysis of catch at site. Size of catch did not vary with site of capture (sites 3 and 4 combined vs. site 2) during the afternoon sampling period (Student's t-test $P=0.2$). The average size of perch >85 mm TL caught by seine did not vary with capture site (Student's t-test $P=0.2$). I am certain that a representative sample of all size classes of perch in the littoral zone, except y-o-y, were collected by seine. No perch longer than 170 mm TL has been caught in Narrow Lake using other sampling methods (trapping, gill netting, angling).

In 1986, 19 seine hauls were done in total during the three day sampling period. On the third day, site 3 was used only once because a large quantity of mud and *Chara* was dragged in by the seine. In June and August 1987, eight seine hauls were made at random from the five available sites (Figure 2.1, sites 2, 4-7) for each sampling day. Three sites were sampled twice per day. By the end of August, rooted vegetation had been completely removed from sites 4 and 7 and the bottom was mud. Sampling at site 4 was moved approximately 30 m north along the shore from the original site. Site 7 was sampled only once per day in August. In 1988 all sites (sites 2-7) were sampled once except site 2 which was sampled twice. A minimum of two hours was allowed between seine hauls at any one site.



Site 1. cobble substrate, few macrophytes
Sites 2, 4, 5, 6. sand and mud substrate with detritus and few macrophytes
Sites 3, 7. thick mats of *Chara* over flocculent sediments

Figure 2.1. Sampling sites for yellow perch at Narrow Lake, Alberta.

Population size and biomass

To estimate fish population size and biomass all fishes caught by seine were measured or counted. In 1986, the perch caught were separated into two size categories: small (<84 mm TL) and large perch (≥85 mm TL). All perch in the large size class were measured to the nearest 2 mm immediately after each seine haul. Perch in the small size class were counted and released except 94 perch (<90 mm TL) which were collected at site 2 at 11:30 on August 27. These fish were killed with an overdose of 2-phenoxyethanol (1-2%) and were stored on ice (maximum 6 h) until measured.

In 1987, all size classes of perch except y-o-y were weighed and measured immediately after capture at the lake except when more than 200 perch were caught in a seine haul. Then weights and lengths were measured only for a subsample of perch (minimum n=30 perch for each 30 mm size class). Only length was measured for the remainder of the perch. Perch <80 mm were either weighed in groups of five or more or were counted.

Perch weighed at the lake were anaesthetized with 2-phenoxyethanol (0.1%) before being measured. Blotted wet weight was measured to 0.01 g with an electronic balance. Total length was measured to 1 mm. The fish were placed in aerated water to recover from the anaesthesia before they were released at the sampling site. When only length was measured, perch were not anaesthetized. Perch which died were stored on ice and remeasured within a day.

The biomass of unweighed perch was calculated for each seine haul from a length-weight regression for perch caught on June 5, 1987 and from length-frequency distributions determined for each sampling period. The biomass of unweighed (but measured for length) northern pike was determined from weights calculated using a length-weight regression of all pike caught during 1987 in Narrow Lake.

Growth dynamics

The summer growth of an age cohort (age 1+) of perch was monitored by collecting perch at two to three week intervals from May to August in 1986, 1987, and 1988. The perch

were collected with a 15 m x 1 m bag seine with 5-mm (stretched) knotless mesh and a 60 m x 3 m beach seine with 5-mm (stretched) knotless nylon mesh. Sampling sites 2, 3, and 4 were used for these collections.

Twenty to thirty perch (<85 mm TL) were collected on each sampling date in 1986. In 1987 and 1988, a minimum of fifty perch per sampling date were collected for measurement and ageing. The maximum size of perch collected included age 2+ perch; therefore, it seems likely that I was collecting the largest size of age 1+ perch. All fish not required for this study were released at the collection site. The perch collected for measurement were killed with an overdose of 2-phenoxyethanol (1-2%), labelled for time and date of catch, and stored on ice until measured. All perch were examined on the day of collection or stored frozen for a maximum of two weeks.

The effect of freezing on the weight and length of perch was tested by individually marking and measuring perch and then freezing them for two weeks. The decrease in weight, -1% (-0.02 g), of the perch after freezing was significantly different (paired t-test $P<0.001$, Appendix 1 Table 2). However, the difference in weight between two measurements taken within one hour of each other was also -1% (-0.02 g) and was significant (paired t-test $P<0.01$). No correction for freezing effects was applied since the variation associated with freezing the perch was not distinguishable from variation in weighing them and was likely the result of drying. The average decrease in total length after freezing was also statistically significant (paired t-test $P<0.001$, Appendix 1 Table 3) but no corrections for changes in length caused by freezing were made.

All perch collected were weighed (blotted wet weight) to 0.01 g with an electronic balance, and total length was measured to 0.1 mm with calipers. Sex was determined by visual inspection of the gonads. Perch with very small and transparent gonads were classified as immature. Male perch, having paired gonads, were usually easily distinguishable from females with their single ovary unless the fish were < 45 mm TL. Perch with larger, whitish colored, vascularized gonads or distinguishable eggs were classified as mature.

Opercular bones were used for ageing, and were removed from the perch after weight and length were measured. The bones were soaked briefly in hot (not boiling) water, wiped clean with paper towel, and stored in labelled envelopes. All perch collected in 1986 were aged in Septmember 1986 using the method of Le Cren (1947). The number of annuli on the opercular bone was counted on the image of the bone projected onto a white wall using a projector with a flat stage (Le Cren 1947). When I was uncertain of the number of annuli, they were recounted the following day. I was uncertain of the number of annuli on opercular bones examined a second time in 10% of the cases. For these perch, the age assigned was taken by counting the annuli on otoliths.

Opercular bones taken from perch collected in 1987 were examined and aged within three days of being removed from perch. They were reaged in the spring of 1988. These bones were aged using a different method. The bones were placed on a black background and the number of annuli were counted using a dissecting binocular microscope with reflected light. Opercular bones of perch collected in 1986 were reexamined using this method. The opercular bones of perch collected during the summer of 1988 were examined within one month of collection, again in the same fashion. The number of annuli assigned to the bones did not differ with the method used or time between removal from the perch and age determination.

Otoliths were taken from all perch collected in 1987 and 1988 and from some collected in 1986. They were used to cross-reference ages determined by opercular bones. The saggitae were most easily removed from the perch from the ventral side. After the alimentary tract is removed from the head region, the otoliths are easily visible through the ventral surface of the brain case. Both otoliths from each perch were removed with pointed forceps after puncturing the skull with the forceps, wiped clean on paper towel and stored in envelopes. Whole otoliths were used to age the perch (Norris 1984). The annuli were best observed when the otoliths were placed in pure glycerin or water and examined under a binocular microscope over a black background using reflected light. Against the dark background, the opaque (summer growth) zone appears white and the hyaline (winter no growth) zone appears as a dark band (Bagenal and Tesch 1978). The growth band (opaque zone) outside the last annulus first appears on

the otoliths of perch from Narrow Lake in June. The otoliths were examined without reference to the age assigned by using opercular bones. The percentage agreement between opercular bones and otoliths was 89% (n=511). The percentage agreement between myself and another individual having experience ageing perch using otoliths was 92% (n=25).

C. RESULTS

Population size and biomass

Approximately 15,000 fish were caught by block seine in Narrow Lake during the sampling periods from August 1986 to August 1988. Yellow perch dominated the fish fauna of Narrow Lake, being the most abundant by number (98.5%) and biomass (62.8%) of the fish caught in the littoral zone (Table 2.1). The overall mean biomass of perch for the three summers of the study was 10.5±3.6 kg/ha (mean±95% C.I., n=42), and their average density in the littoral zone was 3130±1200 perch/ha.

Northern pike was the second most common fish species in Narrow Lake . The overall mean biomass of pike during 1986 and 1987 was 6.2±3.7 kg/ha. The average density of pike was 49±17 pike/ha. The two other fish species in Narrow Lake were burbot, *Lota lota* and Iowa darter, *Etheostoma exile*. Both these species were caught rarely and contributed <1% to the total biomass of the fish population.

Population structure

The perch population in the littoral zone of Narrow Lake was dominated by small individuals less than 80 mm TL and 5 g in weight (Figures 2.2 and 2.3). Perch older than age 4+ were rarely caught, although the oldest perch caught was age 7+. The largest perch caught by seine was 158 mm TL and weighed 38.5 g (n>7000 perch sampled).

In August 1986, one size class of perch (55-80 mm TL) dominated (90% by number) the population structure in the littoral zone (Figure 2.2a). Fewer than 5% of the perch were

TABLE 2.1. Biomass and density of the fish population in Narrow Lake in 1986-1988. All fish were collected between 10:00 and 17:00. No. denotes the number of seine hauls (of 500-m² each) for which biomass and density was calculated. (Number and weight of fish per seine haul is presented in Appendix 1 Table 4).

Date	Biomass (kg/ha ± 95% C.I.)	Population size (No./ha ± 95% C.I.)	No.
Perch			
Aug. 25-27, 1986	18.8±6.4	5560±2100	11
June 2 and 5, 1987	9.4±9.7	3780±3730	11
Aug. 24 and 26, 1987	4.1±1.6	960±340	13
Aug. 23, 1988	10.8±8.8	2290±1820	7
Overall mean	10.5±3.6	3130±1200	42
Pike			
Aug. 25-27, 1986	7.0±8.3	90±30	11
June 2 and 5, 1987	4.9±6.2	12±12	11
Aug. 24 and 26, 1987	7.0±8.3	43±19	12
Overall mean	6.2±3.7	49±17	34
TOTAL	16.7	3180	

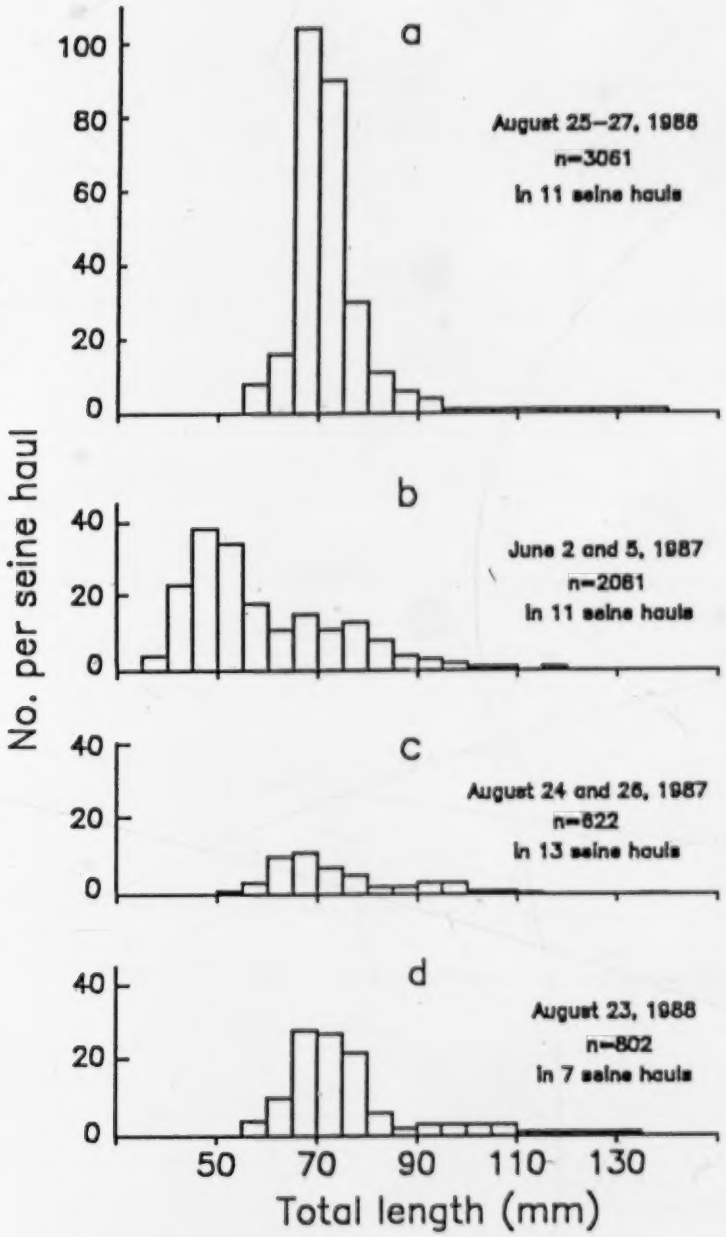


Figure 2.2. Length frequency distributions of perch caught by block seine in Narrow Lake, Alberta, summer 1986-1988.

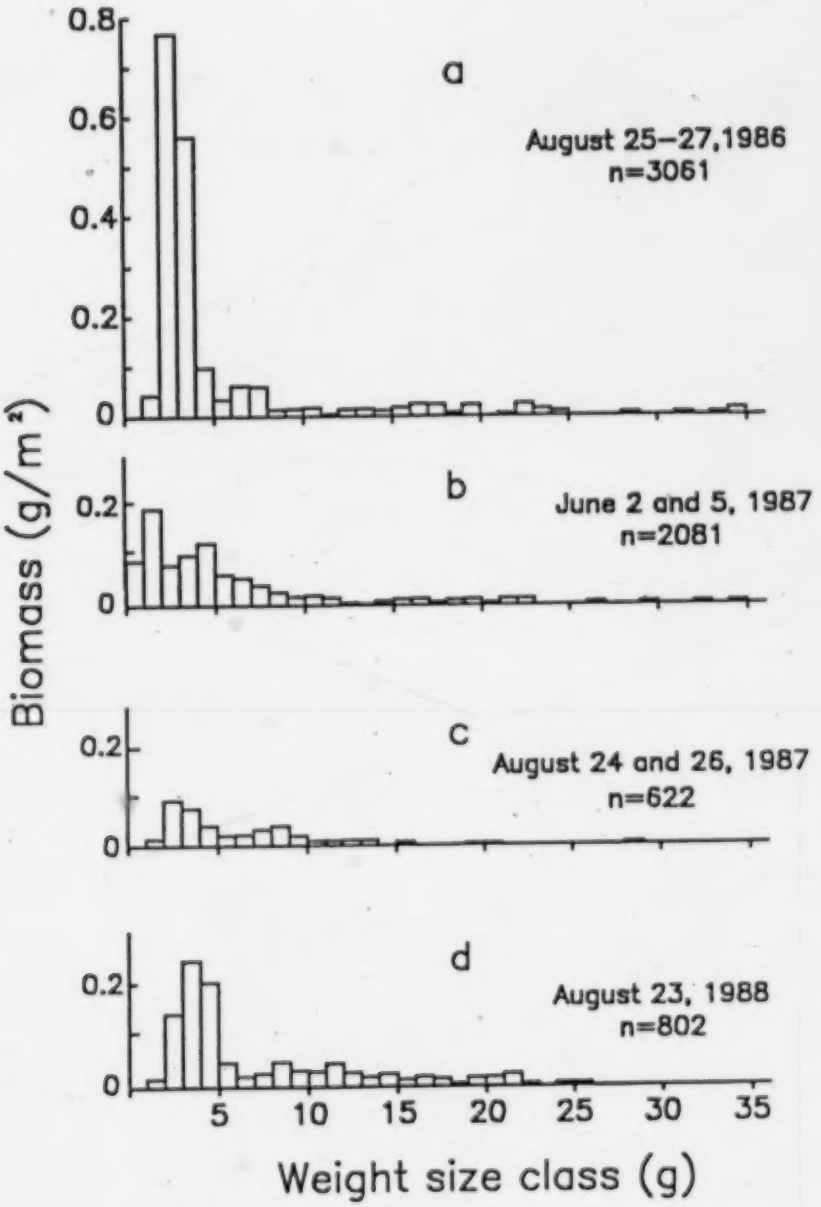


Figure 2.3. Biomass distribution of perch caught by block seine in Narrow Lake, Alberta, summer 1986-1988.

larger than 90 mm TL. The mean size of perch caught in August 1986 was 3.4 g and 70 mm TL (n=3061).

The population was also dominated by perch less than 80 mm TL in August 1987 and 1988. However, this size class accounted for only 75% of the population by number during both summers (Figure 2.2 c and d). Perch larger than 90 mm TL made up approximately 15% of the population. The average weights and total lengths of perch caught in the littoral zone were 4.2 g and 77 mm (n=622) in August 1987 and 4.7 g and 76 mm (n=802) in August 1988.

The size class range in the perch population increased in June 1987 following recruitment of the 1986 cohort to the 35-55 mm size class (Figure 2.2b). This size class accounted for 52% (by number) of the total population size. The smaller catch per unit effort of perch in the next size class, 55-80 mm TL, in June 1987 than in August 1986 reflected high overwinter mortality. Perch abundant in June in the smallest size class (35 to 55 mm) did not progress into the next larger size category (55-80 mm TL).

The biomass structure of the perch population was dominated by perch less than 4 g body weight for all sampling times (Figure 2.3). The contribution of small perch to the total biomass of perch decreased from August 1986 to August 1987 (Table 2.2). Larger perch, 5-10 g, contributed more to the total perch biomass over the same period. In 1988, perch >10 g contributed more to the total perch biomass than this size class had in either 1986 or 1987. Perch >10 g were captured relatively more frequently in 1988 than the two previous summers.

In this population, the majority of individuals are small-sized, resulting in a unimodal population structure. The population structure changes seasonally with an increase in size class range following recruitment of y-o-y in spring. Also, the proportion of biomass in different size classes changed over the study years as larger perch became more important contributors to total biomass. However, the small perch contributed most to the population structure and size throughout the study. The size structure of the population did not reflect the age structure of the perch; the age classes were clumped, for example, size class 0-5 g includes both age 1+ and age 2+ perch. Age 1+ perch contributed most to the population size in all

TABLE 2.2. Biomass distribution and proportion of biomass in weight size categories of yellow perch in Narrow Lake in 1986-1988.

Size interval (g)	Aug. 1986 biomass (kg/ha)	Aug. 1986 freq. (%)	June 1987 biomass (kg/ha)	June 1987 freq. (%)	Aug. 1987 biomass (kg/ha)	Aug. 1987 freq. (%)	Aug. 1988 biomass (kg/ha)	Aug. 1988 freq. (%)
0-5	14.1	78	5.8	62	2.2	53	6.2	57
5-10	1.8	10	2.0	21	1.3	32	1.8	17
10-15	0.6	3	0.5	5	0.4	9	1.5	14
>15	1.7	9	1.2	12	0.2	5	1.3	12
Total	18.9		9.4		4.1		10.8	

three years of study; approximately 80% (by number) of the perch caught in the littoral zone in August 1986 were age 1+.

Mortality

Mortality of juvenile perch was high in Narrow Lake. First year mortality of perch between June 1986 and June 1987 was 0.96 (based on density of y-o-y in June 1986, D. Abbey, pers. comm. and density of age 1+ perch in June 1987). Over winter mortality of the 1985 year-class in 1986-1987 was 0.70 (based on catch per unit effort of age 1+ perch caught in August 1986 and age 2+ perch caught in June 1987). Over summer mortality of age-1+ perch was 0.74 (based on catch per unit effort in June and August 1987). The total annual mortality of age 1+ perch was 92%. The lack of old individuals in the population also indicates high mortality between age 2+ and age 3+ (Figures 2.2 and 2.3).

One source of perch mortality is pike predation. During the summer of 1986, the pike population (7.0 kg/ha) would have consumed a minimum of 131 kg of perch as calculated from the routine metabolic rate of pike during summer (Diana 1979, 1982). This estimate of maintenance ration for pike is equivalent to 30% of the total perch biomass in the littoral zone, or 440 kg. In other words, 30% of the perch biomass could be consumed during the summer by the pike for maintenance alone, with no growth of the pike. This minimum estimate of pike consumption could account for approximately 50% of the summer mortality of the perch.

Growth dynamics

Age 1+ perch did not grow at a constant rate during the summers studied (Figures 2.4 and 2.5). Instead, growth appeared to proceed in stages. During the summer of 1986, the juveniles showed two distinct periods of growth, one in early June and one in August. Virtually no growth in weight (Figure 2.4) or length (Figure 2.5) occurred in July. In June and August, the perch increased in weight 1.8-1.9% of initial body weight per day (Appendix 1 Table 5). From May to August, the perch more than doubled in weight with an overall

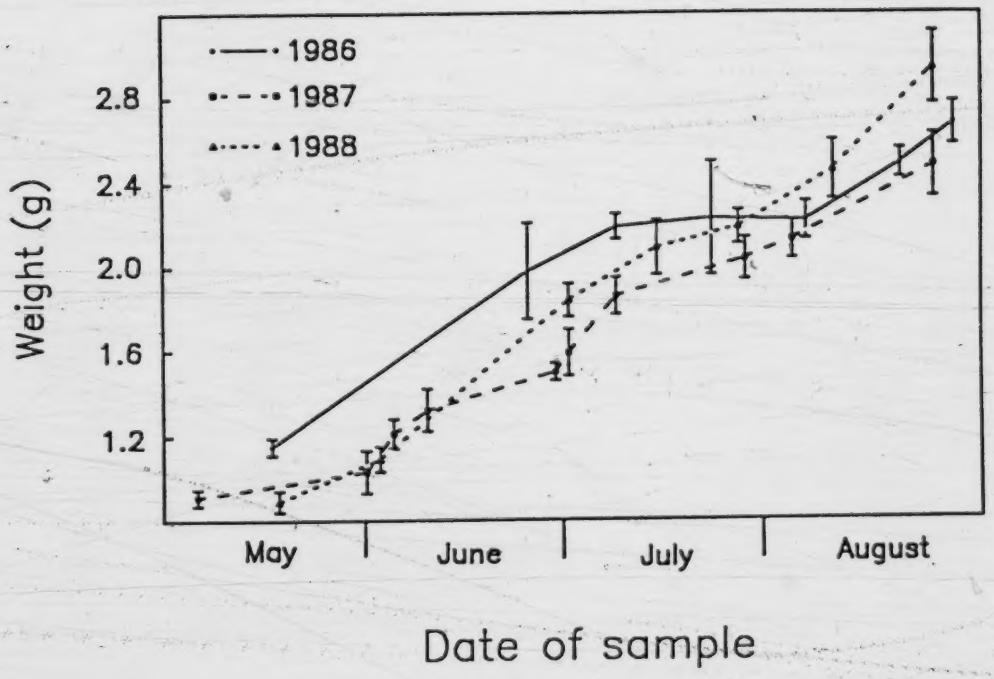


Figure 2.4. Growth in weight of age 1+ perch in Narrow Lake during May-August, 1986-1988. Average weight on any given sampling date calculated from minimum sample size of 17 perch (n=17-86 in 1986, n=58-201 in 1987-1988). Vertical bars indicate 95% C.I.

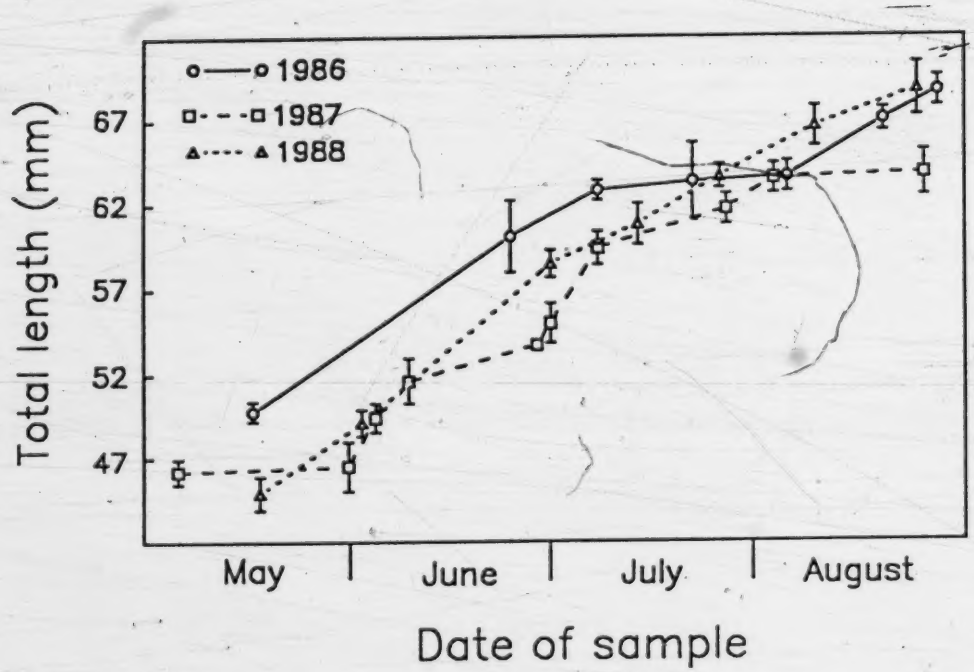


Figure 2.5. Growth in length of age 1+ perch in Narrow Lake during May-August, 1986-1988. Average total length on any given sampling date calculated from minimum sample size of 17 perch (n=17-86 in 1986, n=58-201 in 1987-1988). Vertical bars indicate 95% C.I.

growth rate of 0.015 g/day, or 1.3% of initial body weight per day. They increased in total length 19 mm (38%).

Growth of the age 1+ perch occurred in two types of phases during the summer of 1987 (Figures 2.4 and 2.5). From mid-May to early July and in August the perch grew at 1.8-2.0% of initial body weight per day. The second type of growth occurred in July when growth rate was slower, only 1.1%/day. These perch more than doubled their weight over the summer. The average summer growth rate of the age 1+ perch was similar to the growth rate in 1986, 0.015 g/day, or 1.6% of initial body weight per day. The total increase in length over the summer was 18 mm (35%). The perch gained weight at the end of August but did not show a corresponding increase in length (Figure 2.5).

Growth in weight of age-1+ perch followed the same trend in 1988 as growth in 1987 with a phase of relatively good growth before and after a phase of slower growth (Figure 2.4). In July, the perch grew more slowly (1.6%/day) than in June and August (2.5 and 3.6%/day). Overall, they grew faster during the summer of 1988 than in the two previous years, increasing in weight 0.021g/day (2.4%/day). By the end of the summer, the age 1+ perch had more than tripled their weight. Growth in length was more continuous in 1988 than in 1986 and 1987 (Figure 2.5). They grew 24 mm in total length over the summer.

During each summer of this study growth in weight of age 1+ perch was less in July compared to either earlier in the summer or in August (Figure 2.4). This decrease in growth rate during mid-summer was most prominent in 1986. If age 1+ perch in 1986 had grown throughout the summer at the rate shown in June (1.8%/day), by the end of August they would have weighed 3.17 g, which is 15% heavier than the weight they did achieve. In 1987, had the perch grown throughout the summer at the June growth rate, they would have weighed 2.73 g at the end of August (9% more than their actual weight). In 1988 the perch growth rate decreased from 2.4%/day in June to only 1.6%/day in July. This growth rate was followed by a growth rate of 3.6%/day in August which more than compensated for the slower growth in July.

Growth increment (weight and length) of age 1+ perch was not related to mean water temperature above 12°C (Figure 2.6). Only when water temperature was low in May (Figure 2.7) did growth rate (0.5%/day) appear to be controlled by temperature. No other relationship between temperature and growth was detected. Total summer growth was not related to degree days above 14°C (degree days vs. growth rate: 374 vs. 2.4%/day in 1988; 391 vs. 1.3%/day in 1986; and 438 vs. 1.6%/day in 1987).

Sexual differences in growth of age 1+ perch

Male perch weighed significantly more than female perch at the end of summer during two out of three years of study (Table 2.3). The total length of both male and female perch did not differ significantly except in 1988 when males were significantly longer than females (Table 2.3). Sex ratio of yearling perch was not different from 1:1 (male:female 0.95:1, n=194).

Age 1+ male perch had maturing gonads by the end of August in Narrow Lake. No females at this age had maturing gonads. Only two age 2+ females had maturing gonads in August (n=25) whereas 83% of the age 1+ males had maturing gonads in August (n=41). Within the age 1+ year-class, the maturing males (3.21±0.69 g, 72.0±4.4 mm TL; mean±SD) were significantly larger in both weight and length than the immature males (2.13±0.61 g, 65.2±4.5 mm TL; mean±SD) (one-tailed t-tests, both $P<0.01$).

Length-weight relationships

The relationship between length and weight of the perch studied could be described by the formula $W=aL^3$ (W=weight, L=length, a=constant, 3=slope of the regression line) given by Le Cren (1951) for an ideal fish that maintains one shape as it grows. The regression of log weight on log length using the least square method yielded a best fit straight line which was then used to compare the length-weight relationships between years (Figure 2.8). There was no significant difference between the slopes of the three regression lines for age 1+ perch in August 1986-1988 (ANCOVA $P=0.118$). The slopes of the three regression lines were not

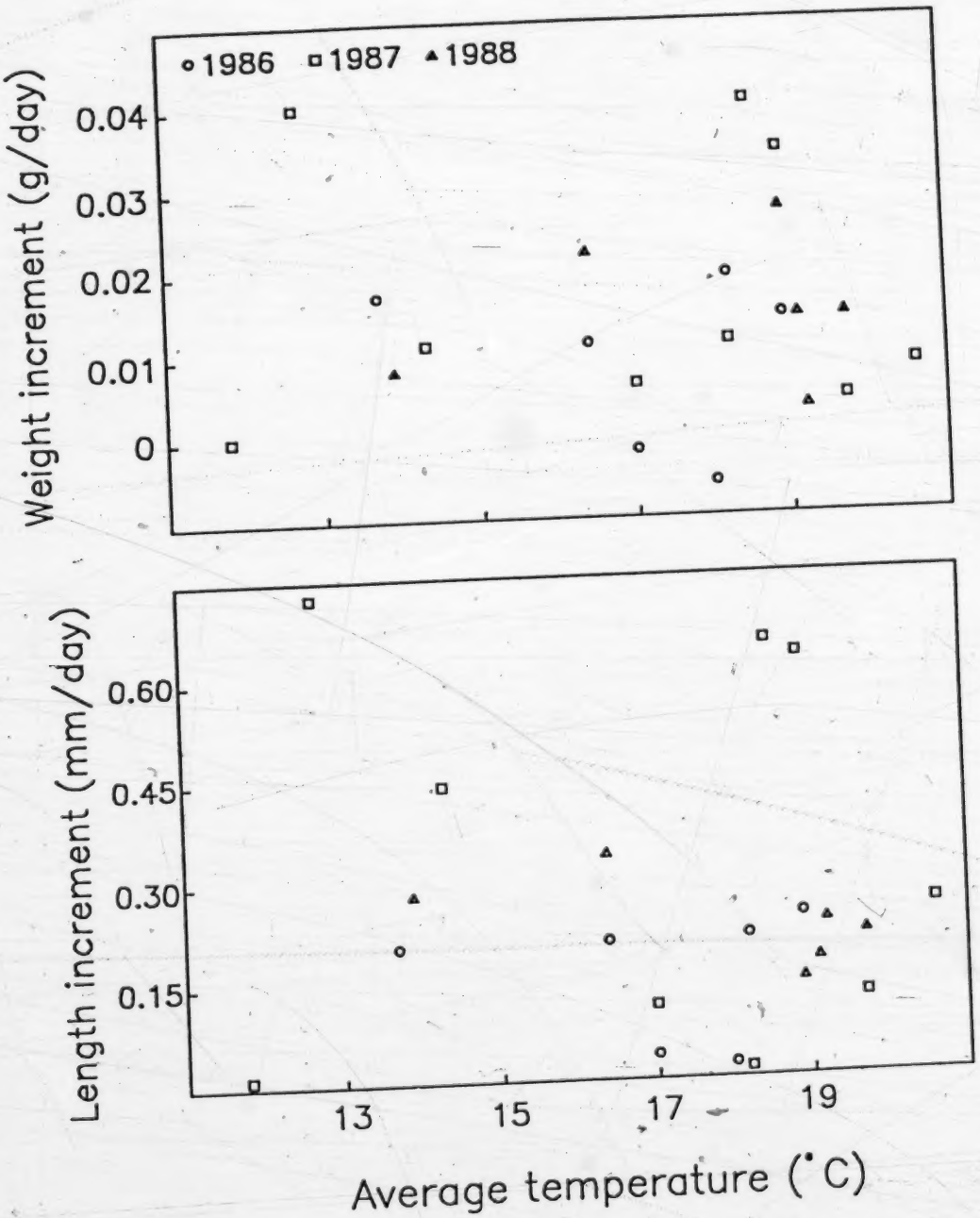


Figure 2.6. Relation between growth increment of age 1+ perch and average water temperature in the littoral zone of Narrow Lake during 1986-1988. Average water temperature (surface to 6 m) was calculated for the time interval between perch sampling dates. Growth increment was calculated as the change in weight or length between sampling dates (g/day, mm/day). Weight-temperature relationship $r^2 = -0.02$; length-temperature relationship $r^2 = 0.13$.

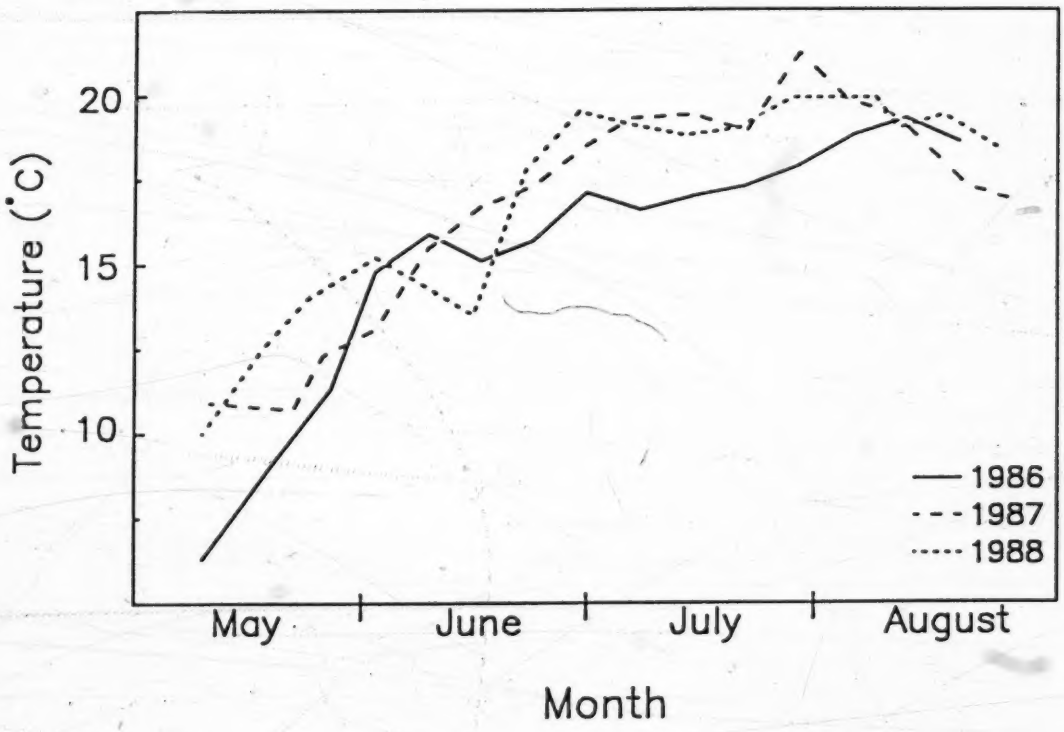


Figure 2.7. Average water temperature in the littoral zone (surface to 6 m depth) of Narrow Lake during May-August, 1986-1988.

TABLE 2.3. Comparison of the average size of age 1+ male and female yellow perch from Narrow Lake in August 1986-1988. Data are given as means±SD and sample sizes are given in parentheses. An asterisk denotes significant values for the one-tailed t-test at P=0.05.

	Sex	Aug. 27, 1986	t-value	Aug. 3, 1987	t-value	Aug. 23, 1988	t-value
Weight (g)	Male	2.81±0.43 (35)	1.84*	2.30±0.42 (33)	1.18 ns	3.11±0.73 (39)	2.29*
	Female	2.63±0.42 (41)		2.17±0.32 (19)		2.72±0.68 (31)	
Length (mm)	Male	69.1±3.8 (34)	0.70 ns	66.0±3.5 (25)	0.73 ns	70.0±5.5 (39)	2.08*
	Female	68.5±3.6 (40)		65.3±2.9 (19)		67.3±5.3 (31)	

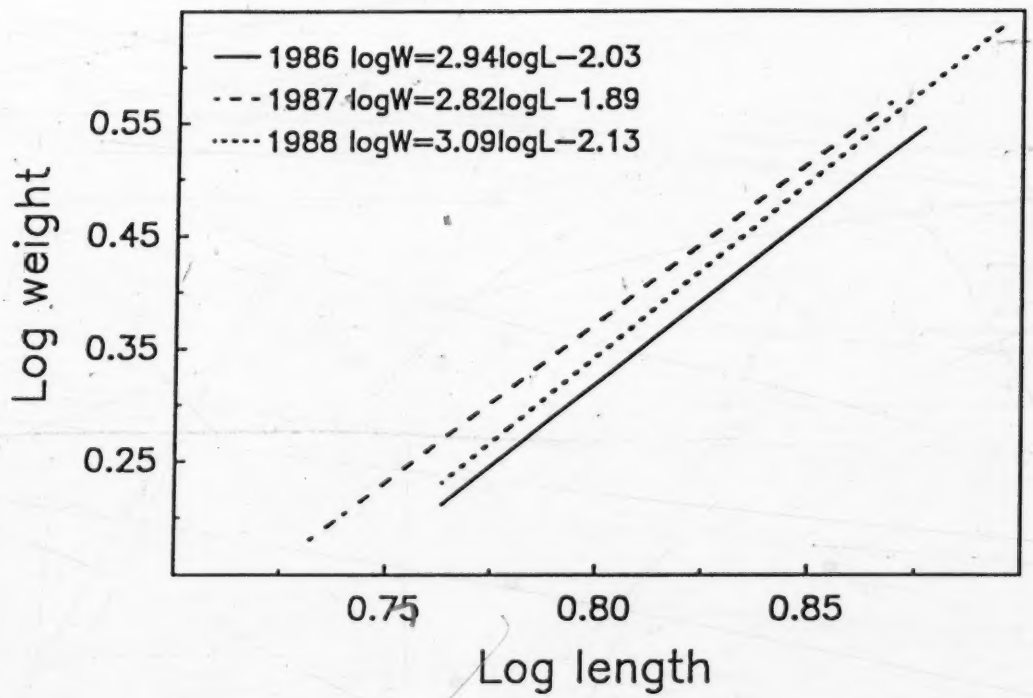


Figure 2.8. Length-weight relationships of age 1+ perch during summer 1986-1988.

significantly different from "3" (1986 slope = 2.94, lower 95% C.I. = 2.71, upper 95% C.I. = 3.17; 1987 slope = 2.82, lower 95% C.I. = 2.59, upper 95% C.I. = 3.06; 1988 slope = 3.09, lower 95% C.I. = 2.95, upper 95% C.I. = 3.23), so perch growth follows the growth pattern described by Le Cren (1951).

When the exponents in the length-weight relationships are equal, the values of the constant obtained in the separate relationships will be a direct measure of condition relative to each other (Le Cren 1951). Therefore, the condition of the age 1+ perch for each year of study was compared using the values of "a" obtained from the regression of log weight on log length. The constant "a" differed significantly between all three years (ANCOVAR $P<0.001$) indicating the condition of the perch differed between summers. The year old perch in August 1987 were significantly heavier at any given length than the same aged perch in 1986 and 1988.

Further analysis of within year differences in condition of the age 1+ perch were carried out using the condition factor calculated by the formula:

$$K = \frac{W*100}{L^3}$$

where K=condition, W=weight (g), L=length (cm)(Le Cren 1951). The condition, an index of well-being, of the age 1+ perch decreased over most of the summers from maxima in May to minima at the end of July throughout the study (Figure 2.9). The condition of the perch had increased by the end of August in 1987 and 1988, but not in 1986.

D. DISCUSSION

Growth

The yellow perch in Narrow Lake are the slowest growing perch of all populations yet examined in Alberta (Figure 2.10). The slow growth rate of these fish is probably partially the function of the shorter growing season of the area compared to lakes in southern Alberta. However, these perch grow slower than those in lakes only a few kilometers away. Compared to the growth of other stunted perch, only perch in one other population grow slower than the perch in Narrow Lake (Table 2.4). The perch in Narrow Lake are the slowest growing perch

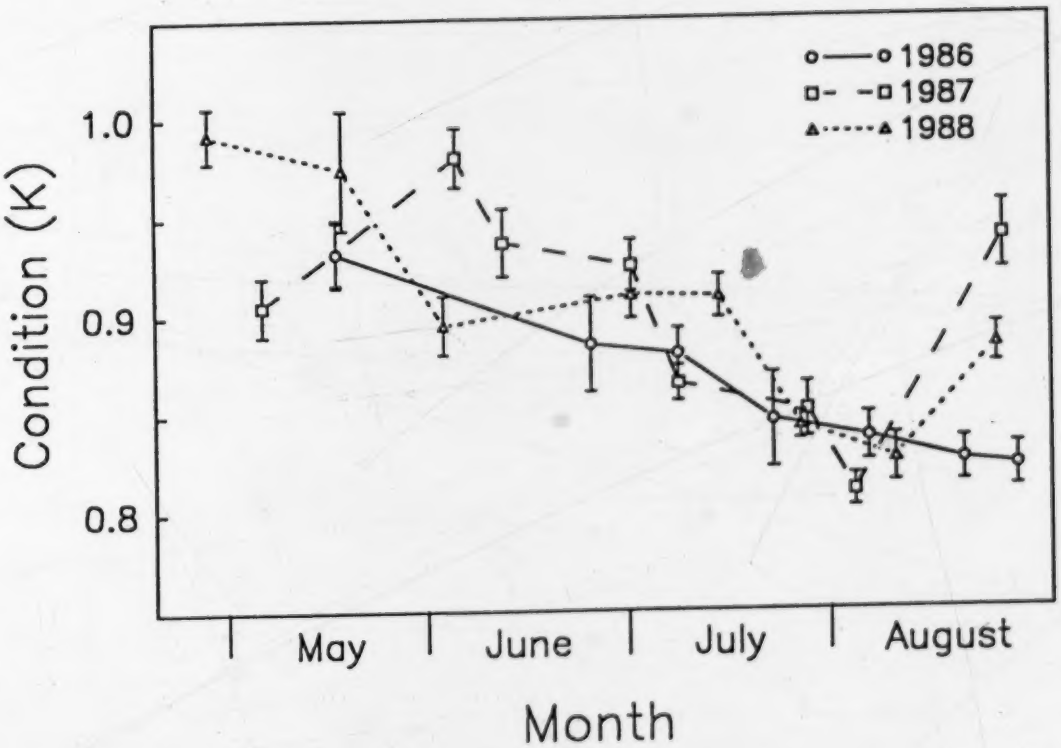


Figure 2.9. Change in condition (K) of age 1+ perch in Narrow Lake during May-August, 1986-1988. Vertical bars indicate 95% C.I. The condition factor was calculated using the formula:

$$K = \frac{W*100}{L^3}$$

where K=condition, W=weight (g), L=length (cm)(Le Cren 1951).

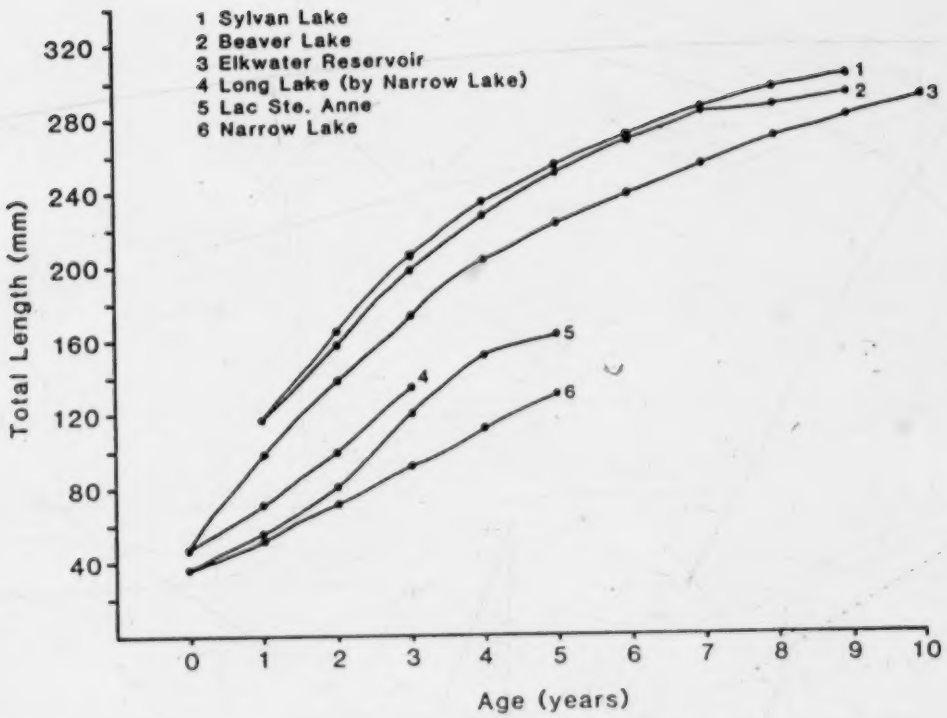


Figure 2.10. Backcalculated total length at age of perch in various Alberta Lakes (W.C. Mackay, unpubl. manu.).

TABLE 2.4. Size at age of stunted perch in various lakes. Total length (mm) was backcalculated using opercular bones.

Lake	Age 1+	2+	3+	4+	5+	6+	7+	8+	Source
Narrow Alberta	52	74	93	112	129				Mackay, pers. comm.
Lac Ste. Anne Alberta	67	88	106	125	142	161			Mackay, pers. comm.
Windemere England	58	105	132	147	157	161	176		Le Cren (1958)
Vinet, Quebec	80	95	115	128	140	145	155		Grimaldi and Leduc (1973)
Hertel, Quebec	68	95	115	127	140	153	164		
Abborrtjärn I, Sweden	78	98	111						Alm (1946)
Horkkajärvi, Finland	63	90	102	111	117	126	133	142	Rask (1984)
Vitalampa Sweden	60	104	127	143	154	165			Nyberg (1979)
Botjärn Sweden	54	85	105	119	130	140	155		Nyberg (1979)
Thompson Montana	48	86	112	142	168				Echo (1955)
Red Deer Ontario	79	128	151	194	213				Chadwick (1976)

reported in the literature for North America and are among the slowest growing anywhere.

Growth of the juvenile perch in Narrow Lake either decreased or stopped in mid-summer in the three years of study. Few other studies have examined growth of an age cohort during the summer and only the study by Nyberg (1979) has found a similar pattern in the growth of adults. He found the growth of stunted perch two years and older in a small Swedish forest lake plateaued during July and August following and preceding periods of relatively rapid growth. However, the growth of younger perch was constant throughout the summer in this population (Nyberg 1979), as was the growth of stunted perch in a small forest lake in Finland (Rask 1984). Variation in environmental conditions, for example, temperature or food availibility, would account for the variable growth rate of the perch in Narrow Lake.

In the present study, there was no relationship between growth increment and water temperature above 14°C or between growth and degree days above 14°C. Positive relationships between growth and water temperature have been observed in other studies (Coble 1966, Le Cren 1958, Neuman 1976). Le Cren (1958) found a positive relationship between degree days above 14°C and total summer growth and a positive correlation between growth increment and water temperature. Temperature controls growth because the rates of food intake, digestion, and metabolism are determined primarily by temperature (Coble 1966). Growth in temperate waters can be described with sigmoid curves showing rapid growth in spring and summer when water temperature is high and growth virtually ceasing in fall and winter when water temperature is low (Allen 1940, 1941). In Narrow Lake when water temperature was low, growth rate of the perch was slow. However, the effects of temperature can be masked by other environmental factors, such as food. In Narrow Lake, growth rate is probably determined by food availability so no temperature-growth relationship is observed. This conclusion is supported by the studies of Coble (1966) and Hokanson (1977) who found no relationship between growth and temperature during the growing season.

Food limitation is the most probable cause of the mid-summer decrease in growth of the age-1+ perch in Narrow Lake. The growth rate of y-o-y perch in Narrow Lake also

decreases in early July compared to growth of y-o-y in nearby lakes (D. Abbey, pers. comm.). Young-of-the-year feed on zooplankton in all the lakes, but in Narrow Lake the age 1+ also feed on zooplankton (Chapter 4). Thus, intense competition between and within the 0+ and 1+ age classes for zooplankton in the littoral zone probably accounts for the observed decreased growth rate of both age classes in July. Persson (1987), using enclosures in Lake Sövdeborg, Sweden, found that zooplankton is a limiting resource for y-o-y perch. On the other hand, Keast (1977) and Rask (1986) suggest the macroinvertebrate feeding stage is critical and that adequate supplies of zooplankton are available in lakes. Obviously this area needs further study but there is sufficient evidence to suggest the hypothesis that zooplankton is a limiting resource in the littoral zone in Narrow Lake.

Nyberg (1979) also suggested that the perch were food limited in the Swedish lake in which the growth of adults decreased in mid-summer. In July, all size classes of perch were consuming zooplankton almost exclusively whereas the larger perch had consumed insect larva and the isopod, *Asellus*, earlier in June when growth was good (Nyberg 1979). He proposed that the larger perch ceased to grow during mid-summer because zooplankton is an inferior food source and is an inadequate energy source for maintaining all metabolic costs including maintanence of growth as in June. Furthermore, since all size classes were feeding on zooplankton in mid-summer, the potential for competition between all individuals was greater. Small individuals, though, can tolerate lower resource levels than larger ones (Werner and Gilliam 1984), as evidenced by their continuous growth during a time when larger fish grew more slowly. Both Nyberg's (1979) observations of slower growth during part of the summer by adult perch, and the growth pattern of young perch during July in Narrow Lake support this hypothesis of food limitation.

Condition

The relative condition of the age 1+ perch in Narrow Lake decreased during the summer to minimum values in July; by the end of August, the perch were either in the same condition as at the begining of summer or were in poorer condition. This pattern follows the

growth rate pattern in Narrow Lake, and is opposite to the pattern observed in other perch populations where condition increases over the summer and autumn, then decreases over the winter (Le Cren 1951, Karas and Neuman 1981). However, the opposite pattern for growth and condition has been observed for trout in streams in the southern United States (Ellis and Gowing 1957, Cada *et al.* 1987). The condition and growth of the trout was lower in the summer and fall than in winter. Cada *et al.* (1987) suggested that limited food supply reduces the growth of young trout in these streams. Rask (1984) found that the perch living under acid conditions in a forest lake in Finland decreased in condition in July and August. The decrease in growth and condition of the perch in Narrow Lake could be the result of inadequate food supply.

Factors such as age and maturity, which are correlated with size, can affect the values for condition (Le Cren 1951). Thus, the variation in condition may be only a function of a size related parameter, such as maturity, that changes over the summer. However, for the age 1+ perch, there was no significant difference in condition between females (immature) and males (mature) (ANCOVA $P=0.26$), indicating that the changes in condition were not a function of maturity. Environmental factors will affect condition. Seasonal changes in condition are often correlated with feeding rate (Le Cren 1951). The change in condition of the young perch in Narrow Lake followed the same pattern as growth rate during the summer. Thus, the decrease in condition during the summer is probably related to food.

Population structure

The perch population in the littoral zone of Narrow Lake was dominated (75-90% by biomass) by fish less than 85 mm TL, which included both age 1+ and age 2+ perch. Not including these small perch in a population estimate would have resulted in a large underestimate of population size. A direct comparison with other population estimates of stunted perch (populations in which all individuals are <16 cm TL) is difficult since most previous studies used collection techniques which selected for mature perch >85 mm (Table 2.5). However, high population density is a common feature of stunted perch (Table 2.5).

TABLE 2.5. Size and biomass of populations of stunted and non-stunted perch in various lakes. Perch were classified as stunted if perch of all ages in the population are < 160 mm TL (based on categories of perch growth determined by Tesch [1955, cited by Thorpe 1977]). Size and maturity of perch used for the estimates is indicated if size was selected for by sampling technique.

Lake	Density No./ha	Biomass kg/ha	Size/Age selected	Source
Stunted perch				
Finnish lakes	3358	51.7	>85 mm	Lappalainen n *et al.* (1988)
13 Finnish lakes	1020	14.0	>age 1+	Sumari (1971)
Horkkajärvi, Finland	1750	23.0	mature	Rask (1983)
Abborrtjärn I, Sweden	2500-3000		mature	Alm (1946)
South Twin, Michigan	2500	5.5		Eschmeyer (1937)
Vitalampa, Sweden	470-950	18-25	?	Nyberg (1979)
Botjärn, Sweden	1590-2890	18-40		
Alinen Mustajärvi, Finland	2700	37.0	>85 mm	Rask and Arvola (1985)
Narrow Lake, Alberta	3130	10.5	>40 mm	this study
Non-stunted perch				
Nimetön, Finland	530	17.0	>2+	Rask (1983)
Ferguson Reservoir, Ohio	300		?	Paxton *et al.* 1981
Red Deer, Ontario	845	8.2		Chadwick (1976)
Memphremagog, Quebec		42.6		Hanson and Leggett (1985)

The average biomass of perch in the littoral zone of Narrow Lake during the three year study was 10.5 kg/ha. The biomass varied from 18.8 kg/ha in 1986, to 4.1 kg/ha in 1987 and 10.8 kg/ha in 1988. This finding is in agreement with the biomass of both stunted and nonstunted perch in a wide range of lakes (Table 2.5). The total fish biomass estimate for the littoral zone of Narrow Lake was 25.8 kg/ha, somewhat lower than the predicted biomass estimate for the lake, 36.3 kg/ha, calculated from total summer phosphorus (Hanson and Leggett 1982).

Year to year differences in year class strength were observed in Narrow Lake. In August 1987, the biomass of perch in the littoral zone was 4.1 kg/ha, 22% of the biomass estimate for August of the previous year (Table 2.1). Removal of y-o-y during 1986 may have contributed to this decline. Between June 3 and July 15, 1986, 367540 y-o-y (22% of all y-o-y) were removed from Narrow Lake (D. Abbey, pers. comm.). Young-of-the-year perch were not sampled in August 1986 so the removal did not affect the biomass estimate in August 1986, but the 1986 perch cohort was included in the samples in 1987. The number of y-o-y perch removed was equivalent to 160 perch/ha, approximately 14% of the total perch population in August 1987 but only 3.5% of the decrease in biomass between 1986 and 1987. The removal therefore accounted for less than 5% of the observed decrease in numbers of the perch population in 1987.

The decrease in population size and biomass of perch in the littoral zone observed between 1986 and 1987 could also be partially the result of destruction of habitat structure by the seine at the sampling sites. Although a small proportion of the total population was sampled (only 15%), the intensive sampling regime may have discouraged perch from feeding at the sampling sites. In 1987, an area of 3.1 ha in the littoral zone was sampled by block seine, and this sampling was concentrated within approximately half a hectare (8 sampling sites at 500 m^2 each). By the end of August, the perch may have used the sampling sites less frequently than adjacent sites. Thus, the decline could be partially the result of an actual change in total population size, or local population depletion at the sampling sites, or the result of changes in perch distribution within the littoral zone caused by destruction of the

benthic habitat. However, the pike biomass estimate was identical in August 1986 and 1987 (Table 2.1). Pike, at least, were apparently using the sampling sites similarily in August of both years. Furthermore, the population was 62% larger in 1988 than in 1987 yet the sampling sites did not appear different during sampling in those years. The decrease in population size and biomass in 1987 can not be attributed exclusively to the intensive sampling regime in 1987. Most probably, however, the perch distribution in the littoral zone changed throughout the study.

There can be substantial fluctuations in year class strength in fish populations depending on spawning success and survival of early life history stages (Forney 1971). Large variations in year class strength of y-o-y perch over the three year study could have had a significant impact on the total population size in Narrow Lake because the population is dominated by one and two year old perch. A weak year class in 1986 compared to 1985 would account for the decrease in total population size in 1987 compared to 1986, especially if mortality is inversely related to population density (Forney 1971). However, in Narrow Lake, the density of y-o-y in 1986 was twice the density in 1985 (D. Abbey, pers. comm.) so the larger 1986 year cohort should have produced a larger population in 1987 than the 1985 cohort could have produced in 1986. Instead, the population size in 1987 was only 22% of the population in 1986. The presence of the 1986 cohort in the population in August 1987 was small (relatively weak <70 mm size class in August 1987 compared to 1986). Again in 1987, the density of y-o-y was only one tenth that of the density in 1986 yet the total population size was almost three times greater in 1988 than in 1987. Although wide year to year fluctuations in year class strength of the y-o-y occur in Narrow Lake, the fluctuations can not account for the change in total population size and biomass structure. However, it does appear that mortality of the y-o-y perch is density dependent.

The size structure and biomass distributions of the perch in Narrow Lake were unimodal, the population being dominated by small, young perch. The population structures of stunted Eurasian perch are unimodal also but dominated by perch between 100 to 130 mm TL when perch are sampled using traps selecting for fish >85 mm (Rask 1983, Rask and

Arvola 1985, Lappalainen *et al.* 1988). Sumari (1971) poisoned small ponds in Finland and collected the dead fish by hand. He determined that the size structure of most populations of stunted perch is unimodal and dominated by perch between 100 and 150 mm TL. Chadwick (1976) used poisoning to unselectively sample all fish in Red Deer Lake, a small Precambrian shield lake in eastern Canada. The yellow perch in Red Deer Lake were slow growing (Table 2.5). The length frequency distribution was unimodal and dominated by small (94% <120 mm TL) young (93% age 1+) perch. A strong cohort needs to appear every one to two years to maintain the population structure observed for the perch in Red Deer Lake. The same pattern in Narrow Lake would maintain the population structure also.

Mortality

The annual mortality of y-o-y perch was 96% and the annual mortality of age 1+ perch was 92%. Mortality rates in other populations of slow growing perch are similar. The annual mortality rate of perch from fry to age 1+ was greater than 99% in a population of perch in Finland (Viljanen and Holopainen 1982). Persson (1983) found 70% overwinter mortality for age 2+ perch and 45% for age 3+ perch in a small Swedish lake. The annual mortality of stunted perch 2+ and older in a Finnish lake was 60% (Rask and Arvola 1985). Approximately 9% of the total fish biomass in the lake studied by Rask and Arvola (1985) consisted of northern pike. Two thirds of the annual perch mortality was estimated to be caused by pike predation (Rask and Arvola 1985). In a similar nearby lake with no pike, the annual perch mortality rate was between 20 and 30%. In Narrow Lake, the high perch mortality, especially between the first and second summers of life, may also be a function of high predation pressure. The pike population contributes approximately 30% to the total fish biomass in the littoral zone of Narrow Lake and therefore should have a substantial effect on the perch population. The proportion of the summer mortality of 1 + perch caused by pike predation, based on a maintenance ration for pike, was 50%.

Cannibalism by the larger perch could also result in high mortality rates of the small perch. In Narrow Lake, adult perch do feed upon the y-o-y perch but only rarely (W.

Jansen, pers. comm.). A few studies have found that older perch eat young perch (Alm 1952, Sumari 1971). Others find that young perch are not important in the diets of older perch (Shafi and Maitland 1971, Rask 1983). The adult perch in Narrow Lake do not appear to exploit the potentially large food source of y-o-y perch.

The result of high mortality is that stunted perch have a short life span in Narrow Lake. Approximately 80% of the population was only one year old and the oldest perch caught was 7+ (n>7000 perch). The reported maximum age of stunted perch is usually 6 to 8 years (Eschmeyer 1937, Nyberg 1979, Rask 1983), although a few studies state that stunted perch lived 10 to 15 years (Alm 1952, Shafi and Maitland 1971). On the other hand, the stunted perch in Lac Ste. Anne, Alberta, rarely live longer than 4 years (W. Mackay, unpubl. data). Nonstunted perch live 9 to 10 years (Scott and Crossman 1979). In Narrow Lake, perch older than four years are rarely caught.

Reproduction

Male perch in Narrow Lake matured at a smaller size (70 mm TL) than male perch in other lakes. Alm (1952) reports stunted male perch were 80 to 110 mm TL at maturity and Shafi and Maitland (1971) report males were 80 to 90 mm TL and females were 110 mm TL at sexual maturity. Generally, stunted fish mature and breed at smaller size than nonstunted fish (Martin 1966, Burrough and Kennedy 1979, Murnyak *et al.* 1984). The size at first maturity for nonstunted perch is usually larger, for example, 100 to 120 mm for males and 200 to 240 mm TL for females (Le Cren 1958, Shafi and Maitland 1971, Thorpe 1974).

The majority of age 1+ male perch in Narrow Lake had maturing gonads in August. In general, the pattern of sexual maturation for other stunted and nonstunted male perch is for maturation to occur at age 2+ and females to mature one to two years older (Le Cren 1958, Shafi and Maitland 1971, Rask 1983). However, Thorpe (1977) reports that the males in some populations of slow growing perch mature at age three, whereas in populations with fast growing perch males mature at age one (Craig 1974, Jellyman 1980). Thus, within some range of growth rates, perch mature at an optimal size (eg. 100-120 mm for males).

Depending on growth rate, the age at which the perch reach 100-120 mm will be one to three years (Alm 1946). When conditions are unfavorable and fish are extremely slow growing and mortality rate is high, they mature earlier in addition to maturing at a smaller size than normal growing fish (Deacon and Keast 1987, Nikolsky 1962 cited by Burrough and Kennedy 1979). However, size continues to play an important role in maturation. In Narrow Lake, the mature age 1+ males were larger than the immature perch. Often, within any year class with both mature and immature fish, the mature fish are significantly larger than the immature fish (Deacon and Keast 1987).

The stunted perch in Narrow Lake mature early at a small size. Such a reproductive strategy ensures high reproductive output and maintains the large population size of young, but sexually mature, perch despite the high mortality rate. In Narrow Lake the perch do not employ the compensatory population mechanisms described by Le Cren (1965) that would enable them to reduce reproductive output and increase growth rate (Jellyman 1980). Instead, the stunted perch have a high fecundity compared to nonstunted perch in nearby lakes (Mance 1987). The reproductive characteristics of the stunted perch are directed towards maximizing reproduction and in this regard the perch population is highly successful. The small perch dominated the population in Narrow Lake, and the success of the population depends on the occurrence of strong year classes at least every two to three years to sustain itself. Year class strength of y-o-y perch did vary approximately ten-fold between 1985 and 1987 (D. Abbey pers. comm.).

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III. EXPERIMENTAL EVIDENCE FOR COMPETITION IN A STUNTED PERCH POPULATION

A. INTRODUCTION

Field evidence for competition in fish populations is mostly deductive and based on observational evidence from uncontrolled natural experiments and whole lake manipulations showing density dependent growth (see Chapter 1). Although such studies support the theory that competition for limited food resources reduces fish growth, direct evidence for competition was not presented. Competition between individuals for an hypothesized critical resource can be demonstrated conclusively if the presence of a potentially competing individual negatively influences some measure of performance such as growth, survival, or fecundity of other individuals (Sale 1979, Connell 1983). Growth, being a sensitive index of available resources, is the best parameter to use to test for competition (Werner and Gilliam 1984).

Several controlled experimental studies provide evidence for competition between fish using growth as the measure of performance. Clady and Luker (1982) stocked yearling largemouth and spotted bass together and separately in artifical ponds in Oklahoma at 250 and 750 fish/ha. The two species grew slower in high density ponds than in the low density ponds in both the monotypic and polytypic assemblages. Bluegill sunfish in small ponds in Minnesota also grew significantly better at low density than at high density (Murnyak *et al.* 1984). Intra- and interspecific competition among and between perch and pumpkinseed sunfish was examined by Hanson and Leggett (1985) using enclosures in a bay in Lake Memphremagog, Quebec. Growth was inversely related to density when the fish were reared separately. When reared together, the perch growth rate was significantly lower than that of the pumpkinseed. They concluded that competition for food is significant at natural perch densities in the lake. Mittelbach (1988) used field experiments to measure competition between juvenile bluegills and pumpkinseeds in Lawrence Lake, Michigan. He found that the growth of both species was inversely related to density. Persson (1987) tested for evidence of

resource limitation for y-o-y perch using field enclosures stocked with the perch and adult roach. Growth of the young perch stocked in enclosures with roach was less than in enclosures lacking roach. Density dependent growth as found in the above experiments provides evidence that the fish are competing.

Stunting is generally thought to be caused by competition. Persson (1983a, b) suggested that intraspecific competition causes individuals to grow slowly and results in a population with limited age and size class diversity. Competition should be greatest between similar-sized individuals. However, there have been no direct experimental tests for intraspecific competition within the dominant size class in populations of stunted perch. The purpose of this field experiment was to test for evidence of competition between juvenile stunted perch in the littoral zone of a lake. The hypothesis tested was that the perch (<80 mm) in Narrow Lake are stunted because they are competing for limited food resources. Growth in weight was used as the measure of performance since body weight is sensitive to temporary changes in food availability (Weatherley 1972).

The experimental approach used was to study the change in growth of juvenile perch using experimental enclosures in the littoral zone stocked at various densities including the natural density of fish in the lake. Under conditions of constant food density, density dependent growth provides evidence that the fish are competing. The experiments included replicate treatments and were repeated over two summers. Downfalls of previous experiments investigating competition among fish, which include lack of replicate treatments (Hanson and Leggett 1985) and excessively high stocking densities (Clady 1981), were avoided.

B. METHODS AND MATERIALS

Enclosure construction and location

I tested for evidence of intraspecific competition among juvenile yellow perch using enclosures in the littoral zone stocked at fish biomasses ranging from 2-15 g/m^2. Eight enclosures (3 x 3 x 1.8 m) were fashioned after those used by Hanson and Leggett (1985).

The frames were constructed with 5 x 10 cm lumber, lined with 1.3-mm mesh fiberglass windowscreen and covered on the outside with 2.5-cm (diameter) mesh chicken wire. The frame bases were made either of 2.5 x 60 cm lumber or of 15 cm galvanized metal sheets (16 gauge) in 3 m lengths. The wooden bases were nailed to the wooden frame and the metal sheets were attached by screws. The cages were bottomless.

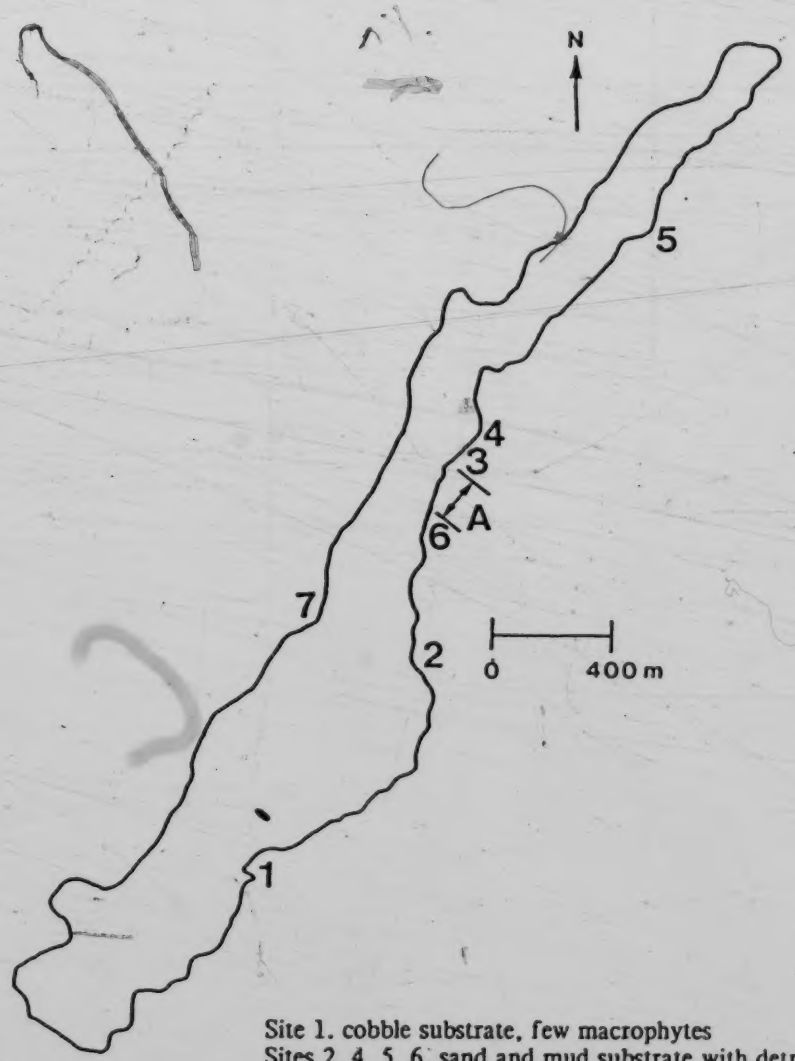
The enclosures were positioned in the lake by pushing the base boards (plates) into the lake sedimets. Concrete building blocks were placed on the corners of each enclosure as weights. All enclosures were checked by divers to ensure that no gaps were present between the enclosure bases and the substrate. Gravel and water-logged logs were placed along the bases in addition to block any gaps. Gill netting (5-cm mesh) was suspended horizontally across each enclosure to discourage avian and human predation (Hanson and Leggett 1985).

The enclosures were aligned parallel to shore between sampling sites 3 and 6 (Figure 3.1) and were spaced 1-2 m apart. The water depth within the enclosures varied between 0.8 and 1.2 m except during the first experiment in July 1986. Then, the water depth was 1.3 m to 1.7 m. The substrate at the experimental site was mud and sand with wood debris and leaf detritus. Approximately 80% of the littoral zone in Narrow Lake has this type of substrate (Hanson *et al.* 1988). The major aquatic macrophytes, *Chara* sp. and *Potamogeton* sp., covered approximately 20% of the bottom area within the cages.

1986 Experimental protocol

In 1986 the perch stocking levels used (5, 10, and 15 g/m^2) were hypothesized to encompass the natural fish biomass of the lake. Narrow Lake has limnological characteristics similar to Lake Memphremagog in Quebec (Pace 1984, J.M. Hanson, pers. comm.), and the measured average fish biomass in the littoral zone of that lake was 12.6 g/m^2 (Hanson and Leggett 1985). Therefore, 10 g/m^2 was used as the preliminary estimate for the total biomass of the littoral zone fish community in Narrow Lake.

Two replicate experiments, each with three treatments (perch biomass 5, 10, and 15 g/m^2) were conducted during 1986, one in July and the second in August (Appendix 2 Table



Site 1. cobble substrate, few macrophytes
Sites 2, 4, 5, 6. sand and mud substrate with detritus and few macrophytes
Sites 3, 7. thick mats of *Chara* over flocculent sediments
Site A. Site of enclosure experiment

Figure 3.1. Sampling sites and site of enclosure experiments in Narrow Lake, Alberta.

1). Three enclosures were positioned on June 28-29, 1986 and allowed to stabilize for two weeks. Treatments were assigned initially at random to the enclosures, and the same treatment was reassigned to each enclosure for the second experiment. One week was allowed between the experiments.

1987 Experimental protocol

Stocking levels used in 1987 were based on a direct measurement of fish biomass in the littoral zone of Narrow Lake. In August 1986, the biomass estimate of fish (>40 mm TL) in the littoral zone was 2.6±1.2 g/m² (mean±95% C.I.). The predicted total lake biomass of fish is 3.12 g/m², based on the relationship determined by Hanson and Leggett (1985) for predicting fish biomass from lake total phosphorus.

Perch densities used as treatments in the first experiment of 1987 were 2, 4, and 6 g/m² (Appendix 2 Table 2). These treatment levels encompassed the measured total fish biomass in the littoral zone in 1986. The stocking levels had no observed effect on perch growth during the June experiment. Because of this result and the high mortality (12-55%, mean=31%) rate during this experiment, higher stocking levels were used (3, 5, and 7 g/m²) in the July and August experiments (Appendix 2 Table 2).

The three experiments of 1987 had four treatments each (0, 2, 4, and 6 or 0, 3, 5, and 7 g/m²) with one replication of each treatment in each experiment. Eight enclosures were positioned during the first week of June and allowed to stabilize for three days. The duration of each experiment was 21-22 days. Between experiments the enclosures were moved approximately 40 m to new sites and allowed to stabilize for two to four days before the next experiment was started.

Stocking and recovery of perch in the enclosures

Perch caught by seine before 12:00 in Narrow Lake were used for the experiment. After capture, the perch were placed in aerated water in plastic coolers. Perch were randomly taken from the holding container, anaesthetized with 2-phenoxyethanol (0.1%), then marked

and measured until the desired stocking level for an enclosure was reached. I marked the perch to distinguish between individuals with intramuscular injections of blue and yellow acrylic paint (Hyplar acrylic polymer plastic color by Grumbacher) near the dorsal fin (Hanson and Leggett 1985). The perch were weighed to 0.01 g (blotted wet weight) using an electronic balance and measured to the nearest 0.2 mm TL with calipers. The marked perch were held in aerated lake water until all had recovered from the anaesthesia, then they were placed in the enclosures. This procedure took approximately one hour per enclosure. For all experiments, two mornings were required to stock the enclosures.

The experimental populations used in the enclosures consisted only of perch between 1.5 and 3.1 g (<80 mm TL excluding y-o-y) (Appendix 2 Tables 1 and 2). This size category was used since it is the dominant size class in the lake and competition should be most intense between similar sized individuals (Persson 1983a). Also, perch typically switch diet from zooplankton to macrobenthos near this size (Clady 1974, Keast 1977) and hence could be most vulnerable to competition at this stage (Hanson and Leggett 1985).

The enclosures were checked daily for dead perch for two to three days after stocking to assess stocking success and to confirm the initital stocking density. I assumed the death of perch within two days of stocking the enclosures was attributable to handling stress. Perch that had died were replaced in the July and August experiments in 1987. For the other experiments when extra perch were not available, the weight of the dead fish was subtracted from the original weight of fish stocked. Therefore, the weights of the perch found dead within two days of stocking were not included in the initital densities reported as the experiment treatments.

The experimental populations were removed from the cages using a 3 x 0.8 m beach seine. One seine haul was usually sufficient to collect the majority of perch in a cage. Other seine hauls were done to ensure all perch were removed from an enclosure. The maximum number caught in subsequent seine hauls was two perch. Removal of all perch from the enclosures required less than one hour and was done between 09:00 and 11:00 for all experiments.

The perch recovered were killed immediately with an overdose of 2-phenoxyethanol (1-2%), placed in labelled plastic bags and stored on ice for two to six hours until measured. Measurements were done in the same manner as described previously. The identifying paint marks were also recorded. Opercular bones and otoliths were taken from each perch for age determination. The entire digestive tract was removed and stored in 70% alcohol.

Growth in weight of perch was used as the indicator of competition between experimental treatments. Therefore, the percent change in weight of each marked individual was calculated and transformed (arcsine transformation) to normalize the variance (Sokal and Rohlf 1969). The means and variances were calculated on the arcsine transformed data and used for statistical analyses (ANOVA). The null hypothesis used was that the change in weight of the individuals should not differ among experimental treatments. Treatments (low, medium, and high perch densities) used for analyses were based on the biomass of perch recovered at the end of the experiments. All data are presented as back-transformed mean weight changes and 95% confidence intervals (CI) for all perch in each experimental treatment.

Growth of the experimental perch was compared to similar sized perch living under natural conditions in Narrow Lake during the same time period as the experiments. The perch collected for the growth study (Chapter 2) were used for the comparison.

C. RESULTS

1986 Experiments

Mortality

The highest observed mortality associated with stocking the enclosures was 8 perch (18%) in one enclosure the day following stocking. Handling mortality was only zero to two perch (0-4%) in the other enclosures for both experiments conducted in 1986.

All marked perch were not recovered for the first experiment of 1986. On July 18 and 19, the lake water level increased by approximately 40 cm and was above the tops of the

enclosures. One unmarked perch was captured in an enclosure which held no marked perch, and another enclosure held eight unmarked perch (Table 3.1). Presumably, perch were able to escape and enter the enclosures during days when the water level was high. Therefore, perch losses to unexplained causes during the experiment were not determined.

Approximately 80% of the perch were recovered from two enclosures in the second experiment (Table 3.1). Perch were not recovered from the third enclosure, instead one pike was captured. The perch were lost either to pike predation or escaped from this enclosure.

Growth

The majority of individuals in the enclosures lost weight during the experiments (Table 3.1). In the first experiment, perch in the enclosure stocked at high density (15 g/m^2) lost significantly more weight, -0.50%/day, than perch in the enclosure stocked at 10 g/m^2 which decreased in weight -0.30%/day (one tailed t-test $P<0.025$). In the second experiment, perch stocked at 15 g/m^2 lost weight at a significantly greater rate (-1.02%/day) than the perch at 10 g/m^2, which decreased by -0.40%/day (one tailed t-test $P<0.001$)(Figure 3.2). Perch under natural conditions in the lake (2.6 g/m^2) grew 0.4%/day during the first experiment and 1.1%/day at the end of August. Perch growth appeared to be inversely related to density (Figure 3.2).

Condition

The condition of the perch in all enclosures decreased significantly during the both experiments (paired t-tests $P<0.001$) (Figure 3.3). The condition of age-1+ perch in the lake also decreased significantly between July 22 and Aug. 19 (Student's t-test $P<0.001$). However, the change in condition of the experimental perch was different between the enclosures. The decrease in condition of perch stocked at 15 g/m^2 was significantly larger than for perch stocked at 10 g/m^2 in both the first (Student's t-test $P<0.05$) and the second (Student's t-test $P<0.001$).

TABLE 3.1. Recovery schedule of perch in two enclosure experiments conducted in 1986 testing for evidence of intraspecific competition. Perch used in the experiments were between 1.5 and 3.1 g (average weight ± SD = 2.34 ± 0.36 g). Losses refers to the number of marked perch lost to unexplained causes during the second experiment. Perch losses in the first experiment were the result of high lake levels and therefore unexplained losses were not calculated.

Experiment	Treatment density	Density Recovered/ (g/m^2)	No. Recovered enclosure	Perch Losses (No.)	No. Gaining Weight
First		Recovery date Aug. 12			
	low	7.4	26*		5
	high	10.4	54		3
Second		Recovery date Sept. 9			
	low	6.8	28	8	2
	high	10.3	49	5	0

*8 perch were unmarked

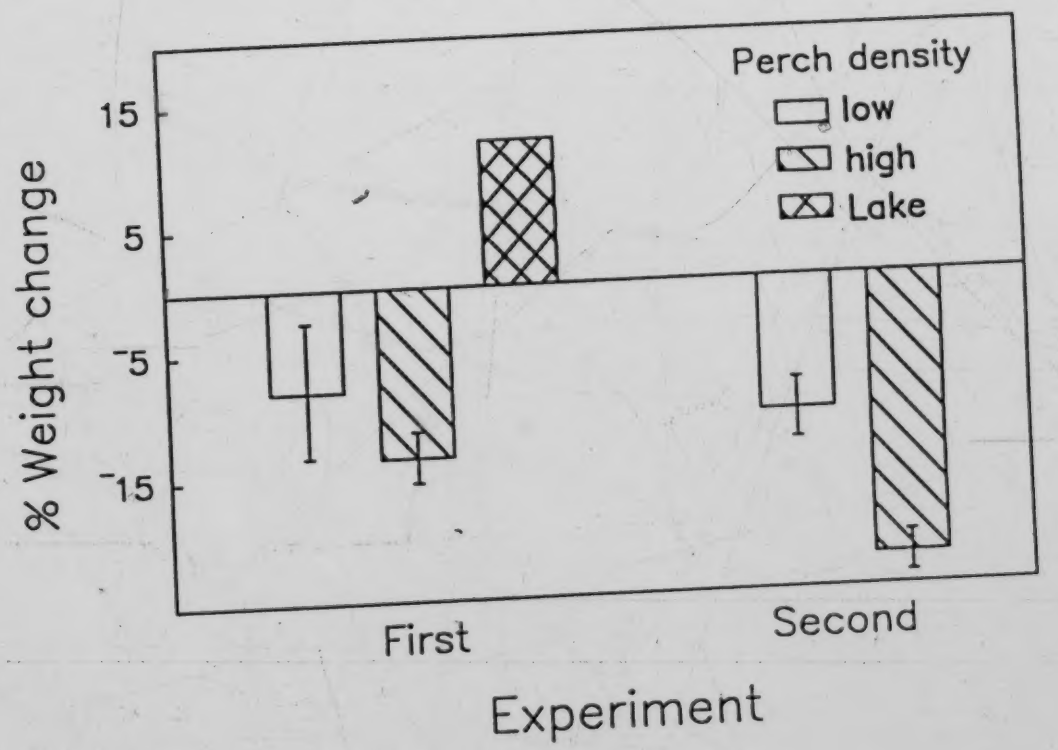


Figure 3.2. Average growth of perch in enclosures at low and high perch densities (6.8-10.4 g/m²) in two experiments conducted in 1986 testing for evidence of intraspecific competition. Duration of the first experiment was 28 days, duration of the second was 21 days. Change in weight of perch from the lake (2.6 g/m²) was over 28 days (collection dates July 22 and Aug. 19). Means and 95% C.I. (vertical bars) of perch in each enclosure are given.

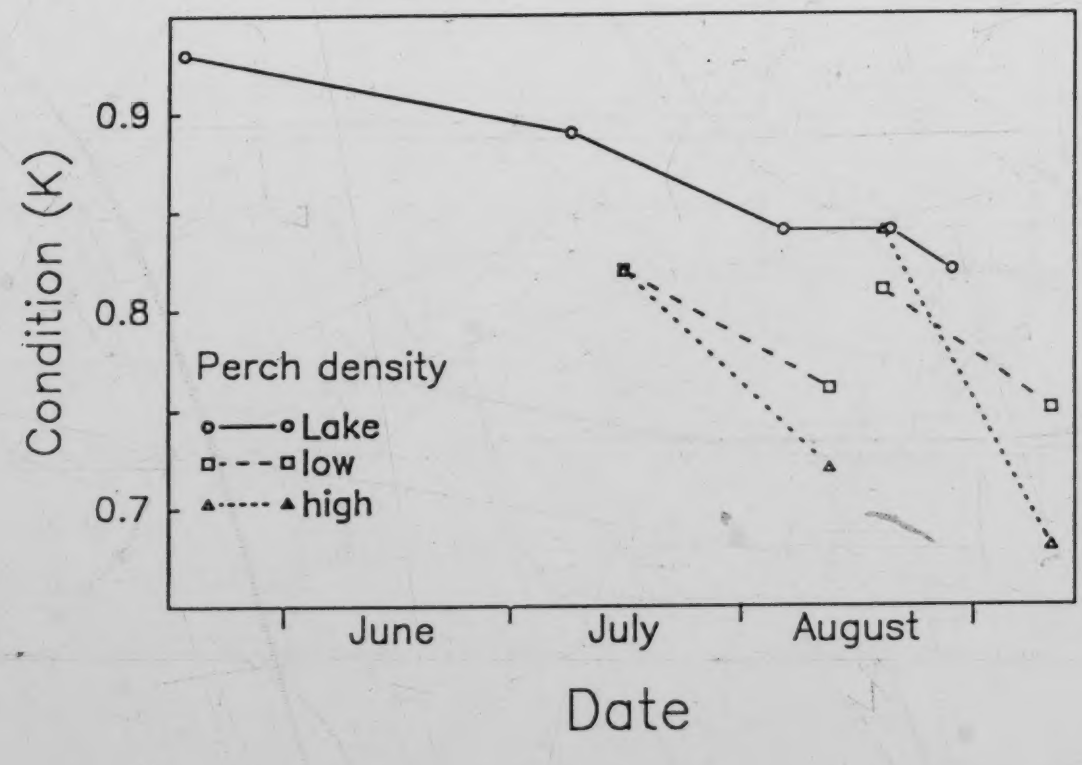


Figure 3.3. Change in condition (K) of perch in the lake (2.6 g/m², solid line) and in enclosures (dashed lines) at low and high perch densities (6.8-10.4 g/m²) in 1986 experiments testing for evidence of intraspecific competition. Duration of the first experiment was 28 days, duration of the second was 21 days.

1987 Experiments

Mortality

Mortality associated with stocking the enclosures in 1987 was highest in the June experiment, at 6%. Five dead perch were observed within one day of stocking the six enclosures. No dead perch were observed within two days of stocking the enclosures for the other two experiments.

Unexplained losses were calculated as the difference between the number of perch stocked and the number recovered. It was assumed that the perch not recovered had died from unexplained causes during the experiment. In the June experiment, 2 to 15 perch were not recovered (Table 3.2). This mortality was not related to perch density.

In the second experiment, unexplained losses were less than in the June experiment (Table 3.2). The highest mortality, five perch, occurred in the enclosure in which a pike was caught. All five perch were probably lost to pike predation since one perch was found in the pike's stomach. Data from this enclosure were omitted from the growth analysis.

Unmarked perch were recovered in five of the six enclosures used in the August experiment. Data from three were omitted from further analyses because there was more than a two-fold difference in the number of perch stocked and the number recovered. Recovery of marked perch in the other three enclosures was 85%.

Growth

In the first experiment of 1987, the mean change in weight in all enclosures was positive (Figure 3.4). Only 36% of individuals lost weight (Table 3.3). Perch growth did not vary with density in the enclosures (ANOVA $P=0.76$). The average increase in weight of the perch in all enclosures was 8.8% ($n=74$, 95% C.I. 12.8 and 4.8) over the duration of the experiment, or 0.42%/day. Age 1+ perch living under natural conditions in the lake increased in weight from 1.32 g to 1.59 g during the same time period, a 20.5% increase during 21 days. Perch in the enclosures (average biomass during the experiment was 3.5 g/m^2) grew less (0.42%/day) than the perch in the littoral zone (0.98%/day) at 1.4 g/m^2.

TABLE 3.2. Recovery schedule of perch from enclosures for which data were obtained for three enclosure experiments in 1987 testing for evidence of intraspecific competition. Perch used in the experiments were between 1.5 and 3.1 g. Losses were the number of marked perch lost to unknown causes during each experiment. The duration of each experiment was 21 days.

Experiment	Density Treatment	Biomass recovered (g/m^3)	Number recovered/ enclosure	Perch Losses (No.)
		Recovery date		
June		July 1		
	Low	1.7	7	3
		2.0	9	2
		1.7	8	10
	Medium	3.8	15	3
		3.2	14	15
	high	5.0	22	6
July		July 29		
	Low	3.2	12	2
		4.0	13	0
	Medium	6.1	25	1
	High	7.0	31	1
		7.0	28	1
August		Aug. 25†		
	Low	3.8	15	0
	Medium	4.1	18	5
	High	6.6	27	6

†Unmarked perch were recovered in 2 enclosures and were included in biomass estimates

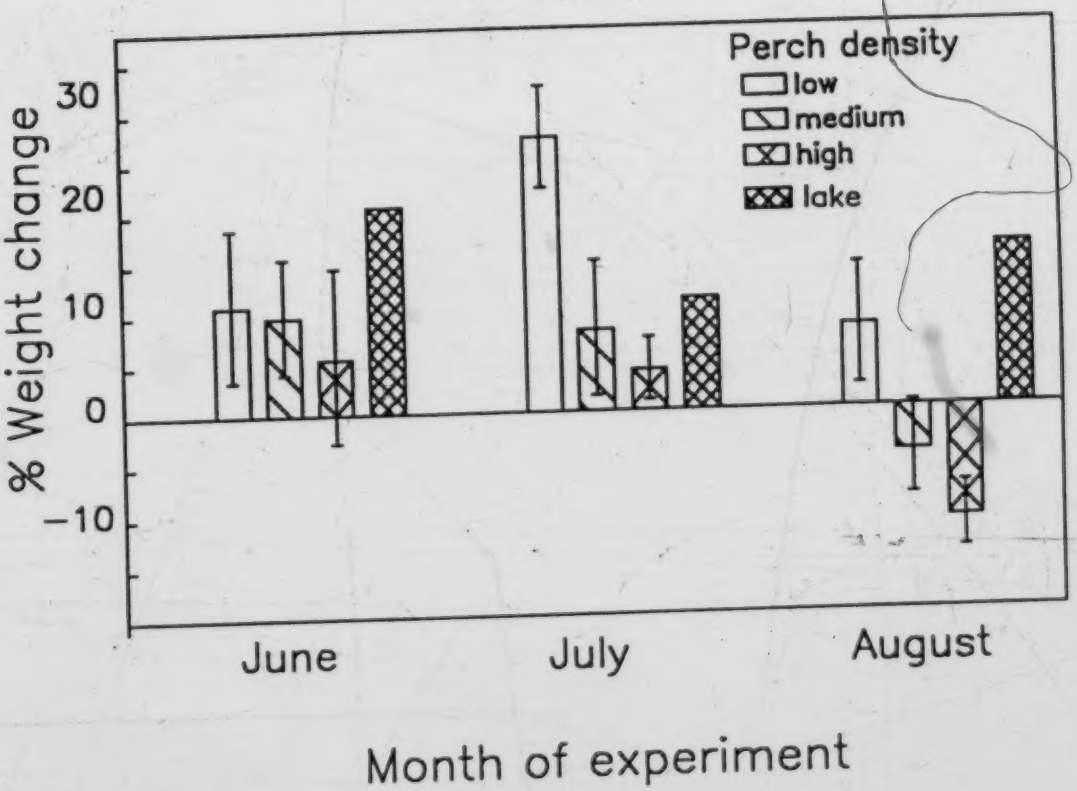


Figure 3.4. Average growth of perch in enclosures at various perch densities (1.7-7.0 g/m ^{2}) in three experiments in 1987 testing for evidence of intraspecific competition The duration of each experiment was 21 days. Change in weight of the perch from the lake (1.1-1.4 g/m^2) was determined using perch caught at the start and end of each experiment. Means and 95% C.I. (vertical bars) of perch in each enclosure are given (perch in enclosures receiving duplicate treatments were pooled). Refer to Table 3.2 for exact densities.

TABLE 3.3. Number of perch gaining and losing weight when stocked at various densities in enclosures in three experiments conducted in 1987 (see Table 3.2 for exact densities). Percentage losing weight refers to the proportion of perch in the enclosures which lost weight during the experiments. The data presented for each treatment include combined replicates.

Treatment (g/m^2)	Number of perch losing weight	Number of perch gaining weight	% losing weight
	June experiment		
2	4	11	27
4	8	15	35
6	15	21	42
	July experiment		
3	0	18	0
5	11	26	30
7	21	31	40
	August experiment		
3	3	11	21
5	12	4	75
7	21	1	96

Perch growth varied significantly with perch density in the second experiment (Figure 3.4). All individuals at low density gained weight during the experiment (Table 3.3). Perch in the enclosures at the higher densities both lost and gained weight, although more perch held at high density lost weight (40%) than at the intermediate density (30%)(Table 3.3). The perch in the enclosures at low density gained significantly more weight (1.29%/day) than perch in the enclosures at higher densities (0.29%/day)(ANOVA $P<0.001$ for both medium and high densities vs. low density). The average change in weight was not significantly different between the perch held at medium and high densities (ANOVA $P=0.20$). Age 1+ perch in the lake increased in weight 0.51%/day during the corresponding time period as the experiment. Perch in the low density enclosure grew more than perch growing under natural conditions in the lake and in the other experimental enclosures. Perch density in the enclosures affected perch growth in July. Perch densities greater than 4 g/m^2 appeared to inhibit growth of perch in the enclosures.

Growth varied with density in the experiment conducted in August (Figure 3.4). Perch in the enclosure at the lowest density, 3.8 g/m^2, increased 8.1% in weight during the experiment (0.39%/day). The majority of perch at medium and high perch densities lost weight (Table 3.3). Perch at the highest density (6.6 g/m^2) lost more weight during the experiment, -0.52%/day, than perch at 4.1 g/m^2, which decreased in weight 0.21%/day. The change in weight of the perch was inversely related to perch density (ANOVA $P<0.001$). Perch in the lake (littoral zone biomass 1.4 g/m^2) grew 0.78%/day during the same time period.

Condition

Figure 3.5 shows the change in condition of perch during the three experiments in 1987. There was no significant change in condition of perch in the enclosures in the June experiment (paired t-tests, all $P>0.2$) and no difference in perch condition between enclosures (ANOVA $P=0.32$). Condition of perch in the lake did not change during the time period between the start and end of the June experiment either (Student's t-test $P=0.3$).

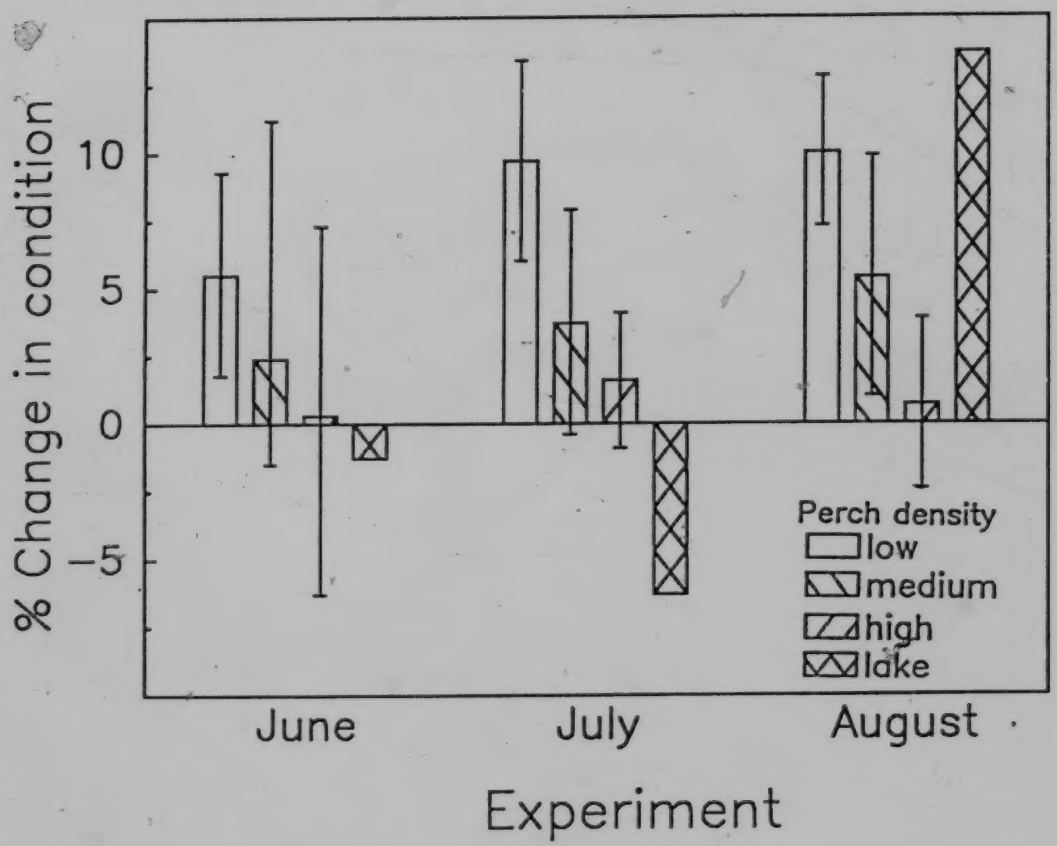


Figure 3.5. Change in condition (K) of perch in the lake and in enclosures at various perch densities (1.7-7.0 g/m²) in three experiments in 1987 testing for evidence of intraspecific competition. Duration of each experiment was 21 days. Change in condition of the perch from the lake (1.1-1.4 g/m²) was determined using perch caught at the start and end of each experiment. Means and 95% C.I. (vertical bars) of perch in each enclosure are given (perch in enclosures receiving duplicate treatments were pooled). Refer to Table 3.2 for exact densities,

The condition of perch at low density increased significantly during the July experiment (paired t-test $P<0.001$). but no change in condition was observed for perch in the other enclosures (paired t-tests, both $P>0.1$). The change in condition of perch was significantly different between the enclosures stocked at low density and both enclosures stocked at higher densities (ANOVA $P=0.005$). The condition of perch in the lake did not vary between July 1 and July 27 (Student's t-test $P=0.1$).

Condition of perch at the low and medium densities increased during the August experiment (paired t-tests, $P=0.01$ and 0.02) as did condition of age 1+ perch in the littoral zone during the same time period (Student's t-test $P<0.001$). Condition of perch stocked at 7 g/m^2 did not change (paired t-test $P=0.5$). The change in condition was significantly different between enclosures (ANOVA $P=0.008$).

D. DISCUSSION

Density dependent growth of stunted yellow perch stocked in enclosures was demonstrated. Manipulating perch density had significant effects on perch growth; perch at the lowest densities gained weight, and perch at higher densities lost weight. Change in condition was also inversely related to perch density. Similar results have been found for growth of nonstunted fish in experimental enclosures (eg. Schneider 1973, Clady and Luker 1982, Hanson and Leggett 1985, Mittelbach 1988). These results provide evidence for intraspecific competition because the presence of large numbers of perch negatively influenced the growth and condition of the individuals, as predicted (Sale 1979, Connell 1983).

Perch stocked in the enclosures at levels approximating the mean total fish biomass in the littoral zone increased in weight, as did the perch living under natural conditions in the lake. In the experiment conducted in July, however, the perch in enclosures at low density grew more than perch living in the lake (1.4 g/m^2). The reason is not readily apparent for the better growth of the enclosure perch. The slower growth rate of perch in the lake during July compared to June or August or perch in the enclosures at low perch density does suggest that resource availability for the total fish population in the lake was less in July than at other

times of the summer. Another possible explanation for the slower growth rate of perch in the lake in July than in the enclosures is that energy expenditure on predator avoidance by perch in the lake could cause a decrease in energy available for growth. The increase in condition of the experimental population also contrasted to the decrease in condition of the perch under natural conditions in the lake at the end of July. The increase in condition also supports the suggestion that energy resources were superior in quality, quantity, or both in the enclosures during the experiment. During July, the y-o-y perch were moving into the littoral zone (D. Abbey, pers. comm.). Possibly the intensity of competition increased in July since growth rates of age 1+ perch (Chapter 2) and y-o-y (D. Abbey, pers. comm.) were lower in July than earlier in the summer.

Mortality in the experimental populations was not related to density of perch in the enclosures. Schneider (1973) found no relationship between survival and final density of yearling perch stocked in experimental ponds. Clady and Luker (1982) found survival was not correlated with intraspecific density of spotted bass in small ponds, but was correlated for largemouth bass. However, since fish growth is a most sensitive index of limited food resources (Werner and Gilliam 1984) and fish will show negaitive growth for extended periods of low food availability (Weatherley 1972), higher mortality rates in response to limited food is not expected for experiments of short duration.

One original intention of the study was to test for increased growth of perch at densities below the littoral zone fish density. Such a test would have conclusively demonstrated that at natural fish densities in the littoral zone of Narrow Lake the perch were competing. However, it appears that the intensity of competition changes during the summer, being highest during July.

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IV. EFFECT OF COMPETITION ON THE DIET OF STUNTED YELLOW PERCH

A. INTRODUCTION

The most widely accepted theory concerning the causes of stunting in perch populations is that competition for food limits the growth of the individuals (Eschmeyer 1937, Alm 1946, Keast 1977, Persson 1983a, 1986). In such populations, the food resources shared by the fish are insufficient to meet the energy requirements for normal growth for the species by all individuals (Wiens 1977). When the demand for food resources by fish is high, not only is the fish population affected, but the prey community may be affected as well.

One effect can be a decrease in abundance or even the elimination of some prey taxa which are selected for by the fish predator (Moermond 1979). For example, Gilinsky (1984) found that densities of *Clinotanypus*, a predaceous chironomid, were negatively related to bluegill sunfish density in cages in the littoral zone of a pond in North Carolina. Hall *et al.* (1970) found that high levels of predation by bluegills caused a decrease in density of the amphipod *Hyalella* and some chironomid species and a decrease in biomass of zygopterans over the summer in small experimental ponds at Cornell University, New York. Bluegill predation in experimental ponds in Michigan altered prey community structure by removing large active invertebrates such as odonates and *Hyalella* (Crowder and Cooper 1982). An increase in the intensity of competition for a preferred prey type by fish, such as perch, which are size-selective feeders (Keast 1977, Wong and Ward 1972), will therefore cause a change in the structure of the prey community by decreasing the abundance of some prey types.

When increased predation pressure on large invertebrates by fish leads to a shift in the size distribution of prey to smaller individuals (Werner and Hall 1979, Werner et al. 1981, Crowder and Cooper 1982, Vanni 1987), smaller prey items will be included more frequently in the diets of the competitors (Crowder and Cooper 1982, Post and Cucin 1984, Hanson and Leggett 1986). The competing fish can respond to the decrease in abundance of preferred prey items by increasing the size range of prey items eaten or by eating prey items not previously eaten (Moermond 1979). Also, at high levels of competition fish have lower consumption

levels (Clady and Luker 1982, Hanson and Leggett 1986). Intense interspecific and intraspecific competition can reduce the quantity of food ingested as well as lead to a decrease in the size of prey consumed. In turn, the decrease in quantity and quality of the diet will result in a depression in growth of the fish.

Small prey items, such as microcrustaceans and plankton, are energetically inferior food items for fish which can use larger prey because net energy intake can not meet the energy demands of maintenance and foraging for small items (Kerr 1971). Diana (1987) calculated that the lack of large-sized prey items (which typically contribute up to 35% of annual ration) in the diet of northern pike could result in stunting. Rainbow trout from populations that consumed a larger proportion of large benthic invertebrates showed superior growth when compared to trout from lakes in which growth was slow (Donald and Anderson 1982). Nyberg (1979) concluded that perch growth in the lakes he studied was limited by an insufficient number of large-sized prey. Konkle and Sprules (1986), based on Kerr's (1971) growth efficiency model, suggested that fish need food items of increasing size as they grow if maximum growth rate and size are to be achieved.

Diet and niche shift studies and resource partitioning studies have often been used to examine the effects of competition between species on fish diet. Werner and Hall (1976, 1979) stocked sunfish (Centrarchidae) at various densities in artificial ponds and observed niche shifts in two species when three species of sunfish were stocked together in the ponds. They concluded that competition for food was occurring and partitioning of habitats was used by the fish as a means of reducing competition. Clady (1981) suggested that the shifts in stomach contents during early summer of two species of bass (*Micropterus*) stocked at high densities in pens in an Oklahoma pond was evidence that competition for food occurred. Hanson and Leggett (1986) found when perch and pumpkinseed sunfish were stocked together in enclosures in a bay in Lake Memphremagog, Quebec, that the perch ate significantly more microcrustaceans than when the perch were reared alone. Persson (1987a) stocked y-o-y perch and adult roach in enclosures in Lake Sövdeborg, Sweden. In the presence of roach, the perch ate macroinvertebrates and copepods whereas when stocked alone the y-o-y fed mainly on

cladoceran zooplankton. The extensive use of detritus and algae by the roach under natural conditions in the lake was thought to be the result of intraspecific competition and competition with perch which caused a shortage of animal food (Persson 1983b, c). The diet shifts and diet segregations between species could lessen the effects of competition for limited amounts of preferred food.

Intraspecific competition between size classes of fish for insufficient amounts of preferred prey such as macroinvertebrates can also result in diet shifts and segregrations. Persson (1987b) found that age 1+ and 2+ perch (mean length 86 and 114 mm respectively) held separately in enclosures in Lake Sövdeborg used the same food resources over the summer. When held together, though, the 1+ perch ate more zooplankton and the 2+ perch consumed more macroinvertebrates. In Lake Horkkajärvi, Finland, the diet of perch in two size classes, 110-130 mm and >130 mm, was dominated by benthic invertebrates at the beginning of summer (Rask 1986). Following a decrease in abundance of benthic animals in mid-summer, the 110-130 mm perch had switched to a diet dominated by zooplankton while the perch >130 mm ate nonbenthic invertebrates such as corixids and water spiders throughout the remainder of the summer. Rask (1986) concluded the decreased availability of benthic food resulted in intraspecific competition between these size classes of perch, which resulted in diet segregation later in the summer. The pattern of diet segregation resulting from competition will depend on differences between the size classes in foraging abilities, in habitat preferences, sensitivity to abiotic factors, and vulnerability to predation (Sale 1979).

When competition for food occurs among fish, one expects to observe a negative relationship between fish density and either the density or biomass of invertebrates and the opposite relationship between fish growth and the availibity of prey (Mittelbach 1988). Mittelbach (1988) found that the growth of pumpkinseed sunfish in cages in Lawrence Lake, Michigan, was positively related to the density of large invertebrate prey at the end of an experiment testing for the effect of competition among sunfishes in the littoral zone refuge. Several studies have found an inverse relationship between fish density and the density of benthic invertebrates (Gilinsky 1984, Post and Cucin 1984, Raess and Maly 1986, Mittelbach

1988) or zooplankton abundance (Vanni 1987). On the other hand, other field experiments have found no relationship between the density of benthic invertebrates and fish density (Clady and Luker 1982, Hanson and Leggett 1986).

Density dependent growth of stunted perch provided evidence that competition was occurring in enclosures in the littoral zone of Narrow Lake (Chapter 3). Information on density dependent growth which demonstrates competition should be supplemented with data dealing with the effects of competition on the critical resource (Sale 1979). If competition is for food, one should be able to demonstrate changes in abundance and composition of the prey for which competition is occurring (Mittelbach 1988). Alteration of the food resource by competition will in turn theoretically affect the competitive interactions between individuals. For example, different size categories of fish could decrease competitive interactions by changing diet or by partitioning resources (Persson 1986).

The purpose of this study was to examine the effects of various levels of competition on quantity of food eaten and food choice by one size class of stunted perch. When macroinvertebrates are selected for by invertebrate-eating-fish, intraspecific competition can result in a bottleneck at the macroinvertebrate feeding level (Keast 1977, Persson 1983a, 1986). Bottlenecks occur when competitive interactions at a specific life stage have significant effects on abundance and size structure of the whole fish population (Persson 1987a). Therefore, the size class of perch used in the study consisted of perch at the stage at which they feed primarily on macroinvertebrates. My working hypothesis was that competition results in a decrease in the quantity of food eaten and a change in the size and type of prey consumed. I tested the hypothesis by examining the diets of stunted perch held in enclosures and subjected to different intensities of intraspecific competition and comparing their diets to diets of perch living under natural conditions in the lake. Comparisons of the diets were made on the basis of abundances of prey types in the stomachs measured using the gravimetric method.

The second purpose of the diet study was to describe the diet, size-related variability in diet, and changes in diet over the summer growing season of the stunted perch (< age 2+)

in Narrow Lake to determine if there is any evidence that food availability or poor food quality (on the basis of prey type) might limit perch growth.

B. METHODS AND MATERIALS

Enclosure experiments

I used experiments with enclosures in the littoral zone of Narrow Lake to establish if differences in the diets of perch were related directly to competitive processes. The stomach contents were collected concurrently with experiments examining the effect of competition on perch growth (Chapter 3). The enclosures were bottomless so the perch could feed freely upon the same organisms as found under natural conditions in the lake. There was a free flow of water and zooplankton into the enclosures in all experiments except during the second experiment in 1986 when the passage of zooplankton (>1.3 mm, size of screen mesh) may have been impeded by accumulation of algae on the screen.

In two experiments in 1986, the perch were stocked in enclosures at densities approximately three to five times the natural fish biomass in the littoral zone of the lake. These perch were between 1.50 and 3.10 g (mean wet weight±SD 2.34±0.36 g, n=150 recaptured). The stocking levels used for the three experiments in 1987 were approximately one to three times the estimated natural fish biomass in the littoral zone of lake (see Chapter 3). The average weight of the perch used in the 1987 experiments was 2.06±0.40 g (n=239 recaptured). The perch were caught and removed from the enclosures at the end of each experiment before 10:30 using a 3 X 0.8 m bag seine.

The diets of perch living under natural conditions in Narrow Lake were examined for size-related variability and temporal changes over the summer. The perch were collected with a 60 x 3 m beach seine. Collections from the lake population were done at two-week intervals from June 28 to August 19, 1986, and at two- to three-week intervals from May 7 to August 24, 1987. Ten to forty perch (1.0-3.5 g) were collected on each sampling date. All perch used for these studies were collected before 10:00.

Sampling protocol for 24-h feeding study

Two 24-h feeding studies were conducted on July 8-9 and August 5-6, 1986, in order to determine the time of maximal stomach fullness so the perch would be sampled at the time of day when stomach contents best represent daily ration. Ten to twenty perch (mean ± SD 2.18 ± 0.47 g, total n = 228) were collected at 3-h intervals, starting at noon, for the two 24-h periods.

Stomach fullness, the measure of food intake relative to fish size, was expressed as the ratio of wet weight of all food in the stomach to wet weight of the fish (mg food/g fish) for each individual (Hyslop 1980). Mean stomach fullness was determined for each sampling time. The data were tested for homogeneity of variances using the F-max test (Sokal and Rohlf 1981). The variances were significantly heterogeneous ($P<0.001$ July; $P<0.001$ August). Therefore, further statistical analyses were performed on the data weighted using the robust general linear model (Kapenga *et al.* 1988). A one way analysis of variance (ANOVA) was used to assess the significance of differences among the amount of prey consumed at each sampling time. A significant result indicated that feeding activity, as reflected by stomach fullness, was discontinuous over time (Jenkins and Green 1977). Scheffe's test for specific comparisons (Prepas 1984) was used to determine the time of day when stomachs were fullest. The time of maximal stomach fullness was morning, and the perch used to examine seasonal and size-related changes in diet were collected between 8:00 and 10:00. Data are presented as the original untransformed data in Figures and both as the original and predicted values based on robust analyses (Appendix 3 Table 1).

Procedure for examining stomach contents

All perch used for the diet analyses were killed immediately after being collected with an overdose of 2-phenoxyethanol (1-2%) and stored on ice until analysed. Perch collected for the feeding chronology studies were frozen for up to two weeks before analyses were done. All other perch were examined within one day of capture.

The guts were removed from each perch after weight and total length were recorded (see Chapter 2). They were stored in 70% ethanol in separately labelled vials until the contents were examined. The stomach contents were examined by slitting the stomach, emptying the contents into a Petri dish, and identifying the prey items with the aid of a dissecting microscope. The various prey items were separated into taxonomic groups, counted, and weighed to the nearest mg using an electronic balance accurrate to 0.1 mg.

The invertebrates most often found in the stomachs of the perch were from the taxanomic groups: Amphipoda (*Hyalella azteca* and *Gammarus lacustris*), Diptera (families Chironomidae and Chaoboridae), Copepoda, Ephemeroptera, Hydracarina, and Trichoptera. Invertebrates found in less than 2% of the stomachs, such as Hirudinae, Hemiptera (Corixidae), Coleoptera (Dytiscidae), Gastropoda, and Diptera (Ceratopogonidae), were classified together as into one prey category, rare prey. Further classification was not done; I assumed that perch do not distinguish between prey items on the basis of species.

Zooplankton and amphipods were difficult to count when partially digested and mangled. Body parts easily identified as representing individual organisms (eg. amphipod heads) were counted. Cladocerans and copepods were especially difficult and time consuming to separate for weighing and counting when partially digested. In these cases, the two taxonomic groups were classified as microcrustaceans and the combined weight of both was recorded.

Analyses of stomach contents for competition experiments

Perch diets were described using the weight and frequency of occurrence methods (Hynes 1950). The relative importance of each major prey item in the stomachs was expressed as the ratio of the wet weight of that prey item to total stomach content wet weight (% mg prey/mg stomach contents). Prey % by weight was calculated for each individual fish and averaged for each treatment. The frequency of occurrence of a prey type was calculated as the number of stomachs containing one or more of a give prey taxa expressed as a percentage of all occurrences of all prey taxa.

The hypothesis tested using the enclosure experiments was that the amount of food eaten by perch will be affected by increasing levels of competition. The amount of food eaten by the perch was expressed as stomach fullness (mg food/g fish). A reduction in stomach fullness is assumed to indicate reduced amounts of food eaten by the perch on a daily basis (Boisclair and Leggett 1985).

ANOVA's were done to assess the effect of fish density on stomach fullness. Variances were significantly heterogeneous before transformation of the data (Bartlett-Box test $P<0.05$; Sokal and Rohlf 1981). The Box-Cox transformation was used to stabilize the variances and normalize the distributions (Sokal and Rohlf 1981) using SPSS-X release 3.0 for IBM-MTS (Anon. 1983). The null hypothesis, that stomach fullness was not different among the treatments (fish densities), was used to test the hypothesis that competition leads to a decrease in the quantity of food consumed. Student-Newman-Keul (SNK; $P=0.05$) tests were performed for any experiments that showed significant effects of density on stomach fullness using an ANOVA so the significant differences could be partitioned among the treatment levels (Prepas 1984). All transformed data were back-calculated for data presentation.

The importance of prey size in the diets of perch in the competition experiments was examined by separating the prey items into two major categories on the basis of size: macroinvertebrates (amphipods, chironomids, ephemeropterans, and rare prey) and microinvertebrates (cladocerans, copepods, hydracarinids). The relative importance of microinvertebrates as a prey item was expressed as a proportion of total stomach contents of each perch (% mg microinvertebrates/mg stomach contents). I tested for any differences in the importance of microinvertebrates in the diets with ANOVA using the Robust General Linear Model (Kapenga *et al.* 1988) with perch density as the treatment. The null hypotheses used to test the hypothesis that competition will cause a change in the size (type) of prey consumed was that the proportion of microinvertebrates in the diets of the experimental perch was not different among the treatments (density). Mean proportion of microinvertebrates are presented as the original data (in Figures) and as both original and predicted values based on robust analyses (Appendix 3 Table 2).

Analyses of stomach contents of perch from the lake

Size-related variability in the diet of perch living under natural conditions in the lake was examined by separating the perch into size categories (≤1.19, 1.20-2.50, and 2.51-4.00 g) for each sampling period. Perch were also separated into size categories so the variability in diet throughout the summer could be investigated. The relative importance (% by weight) of each major prey group and the frequency of occurrence was calculated for each sampling date and size category as previously described for evaluating stomach contents of perch in the enclosure experiments.

Invertebrate collection

Benthic invertebrates were collected so the relation between potentially available prey items, prey eaten, and growth of the perch could be examined and to determine the changes in the number and biomass of the major benthic prey items over the summer. Prey selection by the perch was examined by comparing the proportion of any given prey item in the diet to the proportion of that invertebrate (as a % of total biomass) in the lake and the enclosures.

Data on the biomass of benthic invertebrates in the littoral zone of Narrow Lake in 1986 was obtained from J.M. Hanson, University of Alberta. The same methods were used to collect the invertebrates from the lake and the enclosures. The invertebrate fauna was sampled using a 15 x 15 cm Ekman dredge. The lake benthic collections used for the analyses were done at 2-wk intervals throughout the summer in 1986 at the 1 m depth. Twelve grabs were done on each sampling date in 1986. Five grabs were done at random in all enclosures at the beginning and end of each experiment. Fishless control enclosures (perch biomass 0 g/m^2) were used to test the effect of fish density on macroinvertebrate abundance.

Processing the invertebrate samples involved first washing them on a 500 micrometer sieve. The washed samples were then preserved in 10% formalin in separately labelled glass jars. The invertebrates were sorted by hand, counted, and identified. All individuals of a taxon were weighed to 1 mg. Biomass of the invertebrates was calculated as wet weight (g/m^2). Preserved weights were transformed to fresh weights using conversions determined by

J. M. Hanson (pers. comm.). Data analyses were performed on log-transformed data to test the hypothesis that perch density will affect the biomass of invertebrate prey items in the enclosures. Data presented were backcalculated to the original scale.

C. RESULTS

Twenty-four hour feeding study

Perch < 4.0 g and < 85 mm TL (mean±SD 2.22±0.21 g wet weight, n=121) in Narrow Lake showed significant variation in stomach fullness over the 24-h sampling period in July (Figure 4.1; ANOVA $P<0.001$). The perch collected between noon and 18:00 had significantly less food in their stomachs than individuals collected at any other time (Scheffe's test $P<0.001$), and those collected at 06:00 contained significantly more food than at any other time of the day (Scheffe's test $P<0.001$). The majority of perch caught between noon and 21:00 had empty stomachs. Stomach contents of the remaining perch caught during this time were either partially or very digested, indicating that feeding had occurred earlier in the day (Figure 4.1).

In August, perch (mean±SD 2.13±0.41, n=107) also show significant variation in stomach fullness over the day (Figure 4.2; ANOVA $P<0.001$). Perch collected at 18:00 and 24:00 had significantly less food in the stomachs than perch collected at other times (Scheffe's test $P<0.001$) during the 24-h sampling period. Perch caught at 06:30 had significantly more food in their stomachs than at all other times of the day (Scheffe's test $P<0.001$). The majority of perch with empty stomachs were caught at times of day when stomach fullness was lowest. Perch appeared to feed both in the evening and morning in August, although stomachs were not as full in the evening as in early morning.

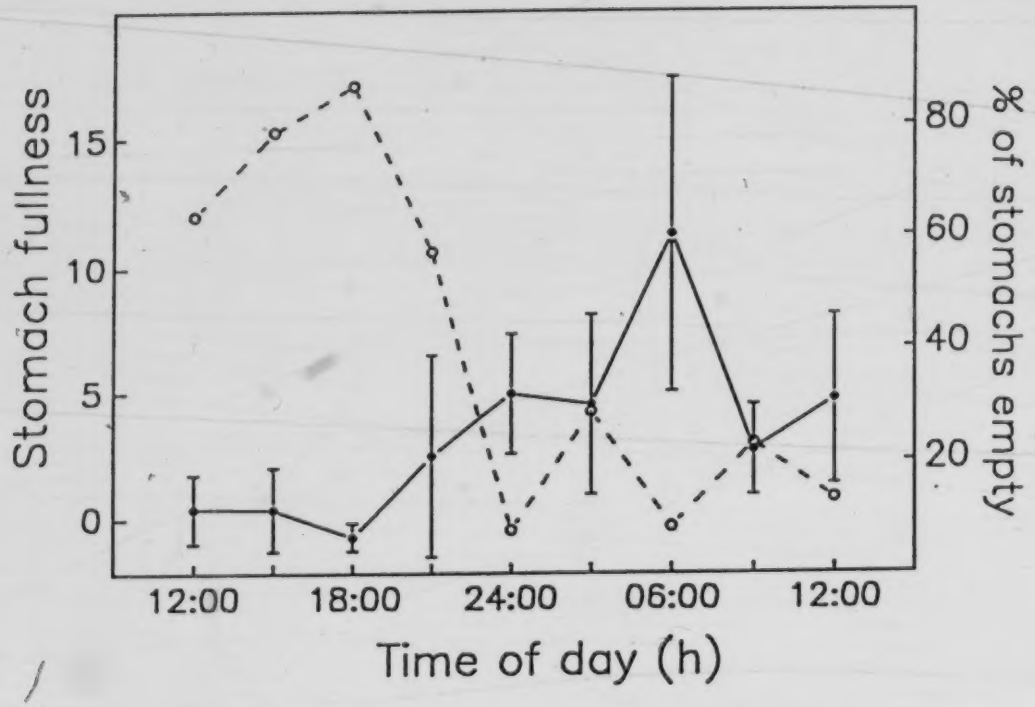

Figure 4.1. Stomach fullness (mg food/g fish), solid line, and % of perch with empty stomachs, dashed line, for perch (<85 mm TL) in Narrow Lake during 24-h sampling on July 8-9, 1986. Each value is the mean at each sampling time (range n=11-15, total n=106). Vertical bars indicate 95% C.I.

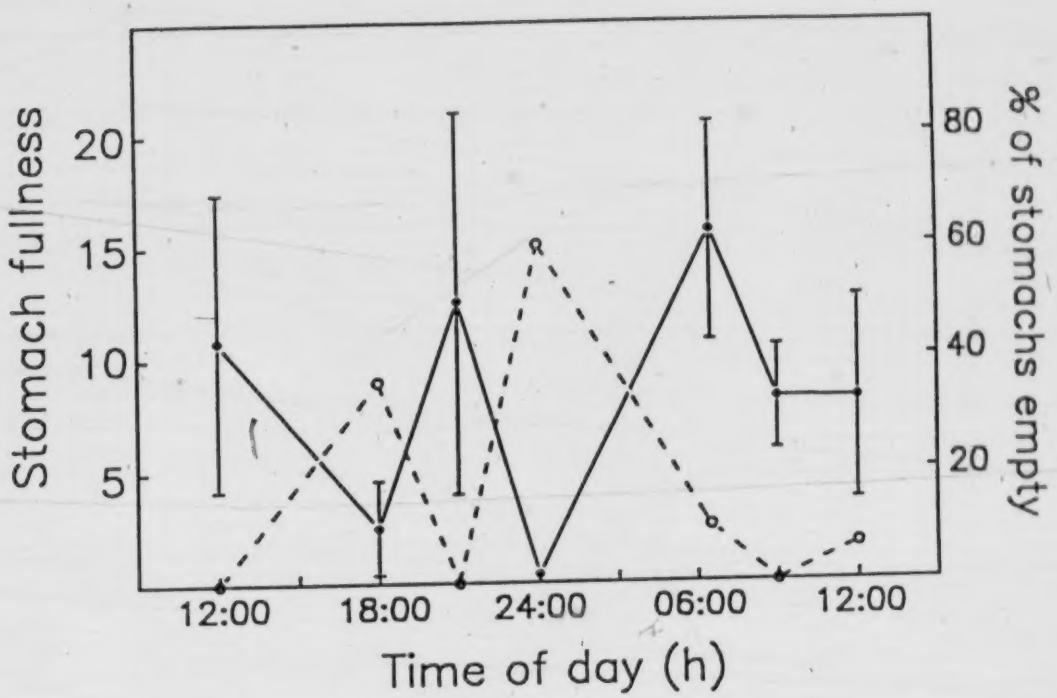

Figure 4.2. Stomach fullness (mg food/g fish), solid line, and % of perch with empty stomachs, dashed line, for perch (<85 mm TL) in Narrow Lake during 24-h sampling on August 3-4, 1986. Each value is the mean at each sampling time (range n=12-20, total n=107). Vertical bars indicate 95% C.I.

Stomach contents of perch from the lake

During the summer of 1986, cladocerans were the prey most important (by weight) in the diet of perch <4.0 g and 85 mm TL (Table 4.1). Cladocerans were also the dominant prey item in the diet of the smallest size class of perch (1.20-2.50 g body weight), both in terms of weight (62.5%) and frequency of occurrence (74.1%) (Table 4.1). The larger perch (2.51-4.00 g) ate cladocerans less extensively than smaller perch over the summer (only 34.8% by weight). Although cladocerans were the dominant prey item by weight for the larger perch, amphipods were found more frequently than cladocerans in the stomachs. Other invertebrates found in the perch stomachs were corixids, chironomids, coleopterans, hydracarinans, copepods, and trichopterans. Larval fish (Iowa darters and y-o-y perch) were found in the stomachs of the larger perch more frequently than in the stomachs of the smaller perch.

Variation in diet of perch over the summer in 1986 is shown in Figure 4.3. At the end of May, the major prey item (by weight) for the smaller perch was chironomid pupae (Figure 4.3a). Mayfly larvae and chironomid pupae were equally important in the stomach of the larger perch at the end of May (Figure 4.3b). The most notable trend in the diet of the larger perch was the increase in contribution of amphipods to total stomach contents until July which was followed by a dramatic decrease. Then, the importance of amphipods in the diet decreased and more cladocerans were eaten. Cladocerans increasingly contributed to the diet of the smaller perch throughout the summer until by the end of August they dominated the stomach contents (on a weight basis). At the end of August, perch of both size categories were feeding predominantly on zooplankton.

During the summer of 1987, the perch (<4.0 g and 85 mm TL) ate mainly amphipods and cladocerans (Table 4.2). The smallest perch (0.50-1.19 g), caught between May 7 and June 10, fed almost exclusively on chaoborid larva and cladocerans. The largest category of perch (2.51-4.00 g) ate more amphipods, both by weight (46.6%) and occurrence (47.9%), than the medium size perch (1.20-2.50 g) during the summer (24.7% by weight, 36.6% by occurrence). These medium-sized perch ate more cladocerans. Chironomids were eaten less frequently by the medium-sized perch and more frequently by the larger perch in

TABLE 4.1. Stomach contents of two size classes (1.20-2.50 g and 2.51-4.00 g) (means±SD are presented) of perch in Narrow Lake, expressed as percentage by weight [(mg prey item/mg total stomach contents)*100] and as frequency of occurrence (number of stomachs containing a prey group as a percentage of the total number of stomachs). Perch were collected from June to August, 1986. Only prey occurring in more than 1% of all stomachs are itemized separately. Rare prey items were corixids, trichopterans, and coleopterans.

Prey group	"small" perch (1.92±0.42 g) n=81		"large" perch (3.28±0.41 g) n=45	
Prey group	Weight	Freq.	Weight	Freq.
Amphipods	17.2	24.7	23.5	48.9
Chironomids	12.3	21.0	13.5	26.6
Cladocerans	62.5	74.1	34.8	42.2
Ephemeropterans	0.4	2.5	8.5	6.6
Fish	7.2	6.2	19.1	6.7
Rare prey	0.4	4.9	0.6	8.9

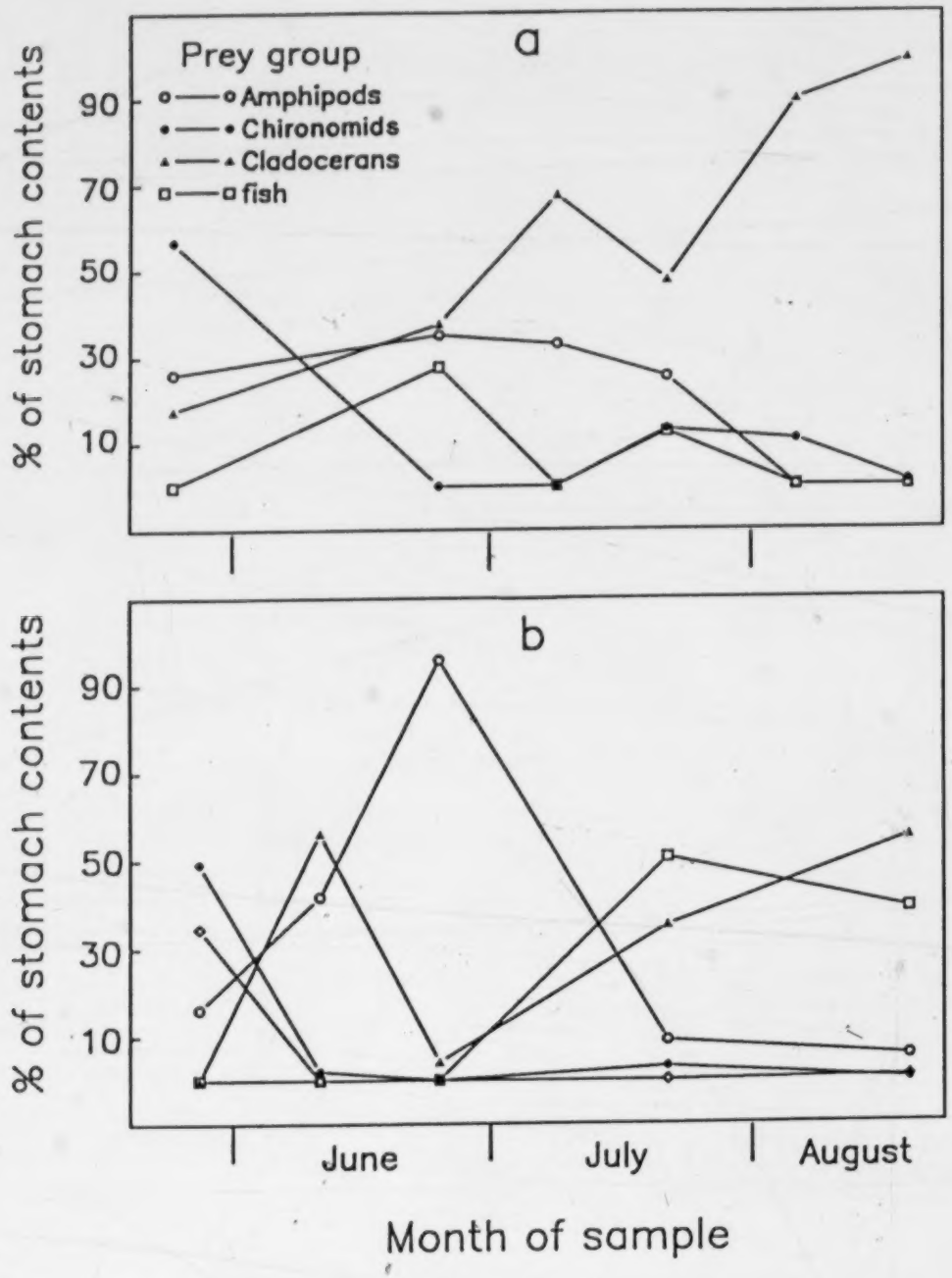

Figure 4.3. Summer % composition (by weight) of the diet of two size classes of perch (a 1.20 to 2.50 g and b 2.51 to 4.00 g wet weight) during 1986 in Narrow Lake. Stomach contents were calculated as [(mg prey item/mg stomach contents)*100] (range n=7-20 on any given sampling date).

TABLE 4.2. Stomach contents of three size classes (≤1.19, 1.20-2.50, and 2.51-4.00 g) (means ± SD are presented) of perch in Narrow Lake, expressed as percentage by weight [(mg prey item/mg total stomach contents)*100] and as frequency of occurrence (number of stomachs containing a prey group as a percentage of the total number of stomachs). The smallest size category of perch was collected in May and June, 1987. The other sizes of perch were collected from May to August, 1987. Only prey occurring in more than 1% of all stomachs are itemized separately.

Prey group	"small" perch (0.85 ± 0.23 g) n=29		"medium" perch (1.79 ± 0.40 g) n=71		"large" perch (3.21 ± 0.37 g) n=71	
	Weight	Freq.	Weight	Freq.	Weight	Freq.
Amphipods	0	0	24.7	36.6	46.6	47.9
Chironomids	0.3	6.9	5.6	23.9	18.4	40.8
Cladocerans*	37.9	51.7	48.9	56.3	13.1	36.6
Chaoborids	61.8	58.6	9.1	16.9	13.0	19.7
Fish	0	0	6.6	2.8	7.3	4.2
Rare prey†	0	0	5.0	25.3	1.2	16.9

*on Aug. 4 this prey group included copepods for the two size classes
†including corixids, ephemeropterans, trichopterans, and coleopterans

1987 than in 1986. More "rare" prey items were found in the stomachs of perch in 1987 than in 1986, although they did not contribute substantially to the diet either in terms of weight or frequency of occurrence.

Composition of the diet of perch over the summer in 1987 is shown in Figure 4.4. Greater than 70% (by weight) of the prey eaten by the smaller size category of perch were midge larva (Chaoborinae) in May. Chaoborinae larvae were less important in the diets of the next larger size catergory (<30% by weight). Chironomid pupae were the dominant item in the stomachs (67% by weight) of the largest size category of perch in May, making up approximately 70% of the diet. In June, amphipods and cladocerans dominated the diets of both size clases of perch. From July to the end of August, variation in the diets of the perch was mainly the result of changes in the weight of amphipods and cladocerans eaten. Cladocerans increased in importance and amphipods decreased in importance over July and August in the small size class (Figure 4.4a). Compared to 1986, amphipods appeared to be more important in the diet of the largest perch at the end of August, 1987.

In 1986, stomach fullness of the larger perch (2.51-4.00 g) varied over the summer (Figure 4.5; ANOVA $P=0.02$). Stomach fullness of the perch at the end of June was significantly less than the stomach fullness of perch caught at the beginning of June and the end of July (SNK). No changes in stomach fullness of either size category of perch was observed in 1987.

Invertebrate prey availability

Changes in the proportion of amphipods in the stomachs of perch (Figure 4.3) occurred near the time when the biomass of benthic invertebrates in the littoral zone of Narrow Lake decreased in summer, 1986 (Figure 4.6). The total biomass of benthic invertebrates decreased in July (Figure 4.6), amphipods showing the most dramatic decrease (Figure 4.7). The proportion of amphipods in the stomachs of perch (2.51-4.00 g) decreased from the end of June to July (Figure 4.3b). Cladocerans contributed more to stomach contents than amphipods throughout the remainder of the summer in both size categories of

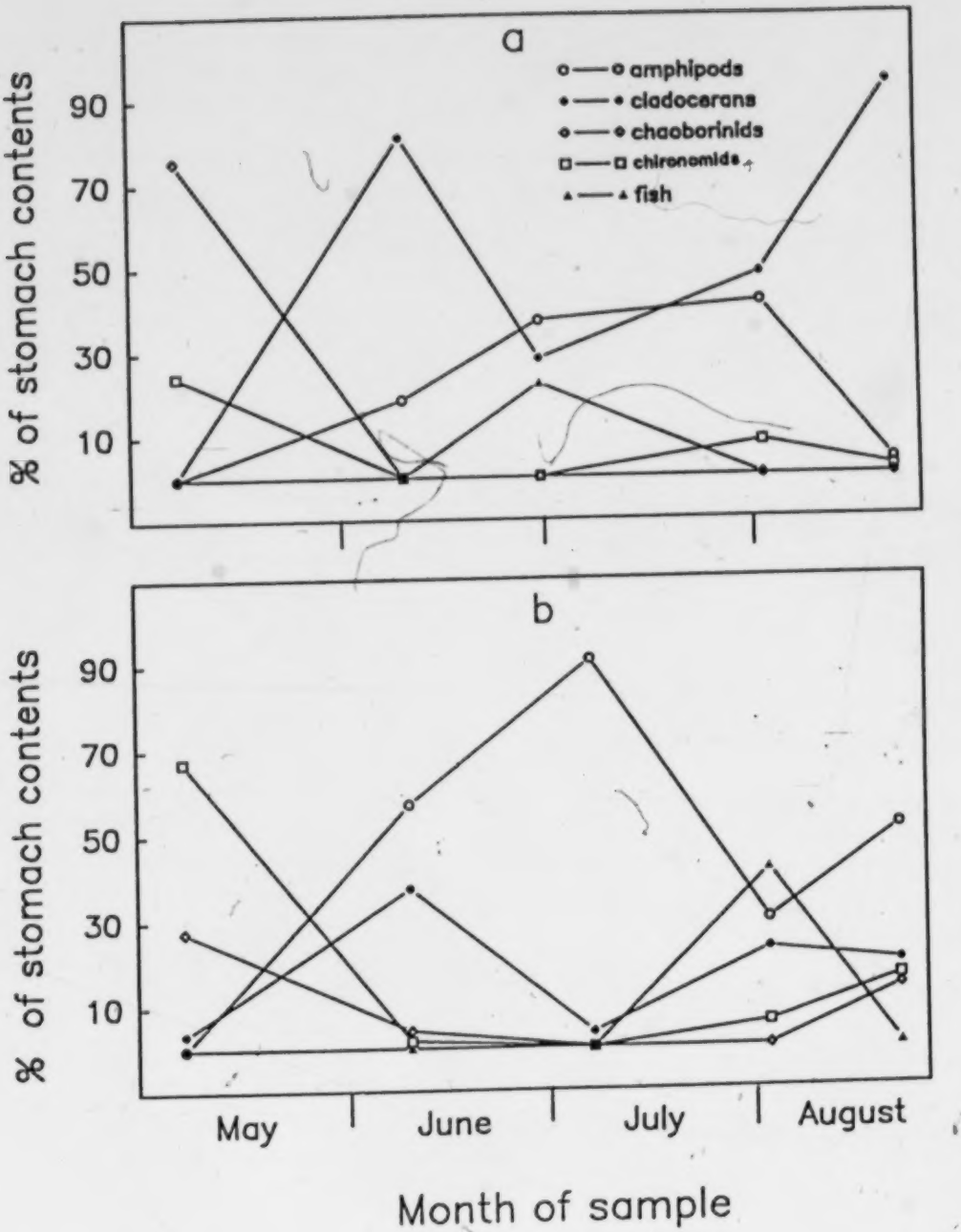

Figure 4.4. Summer % composition (by weight) of the diet of two size classes of perch (a 1.20 to 2.50 g and b 2.51 to 4.00 g wet weight) during 1987 in Narrow Lake. Stomach contents were calculated as [(mg prey item/mg stomach contents)*100] (range n=10-18 on any given sampling date).

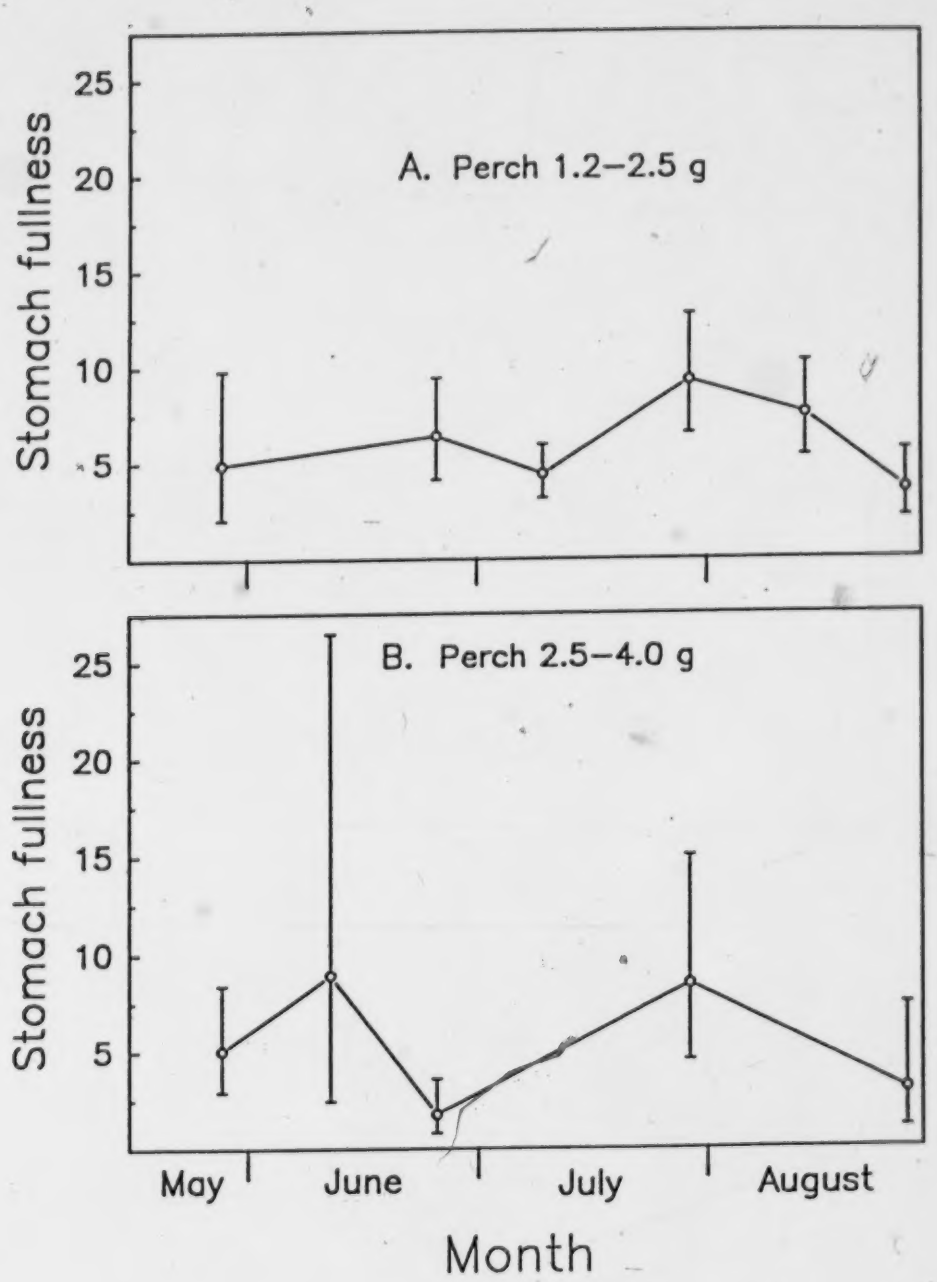

Figure 4.5. Stomach fullness (mg food/g fish) of two size classes of perch (1.20-2.50 and 2.51-4.00 g wet weight) during May-August, 1986 in Narrow Lake. Each value is the mean of 7-20 perch sampled on each date. Vertical bars indicate 95% C.I.

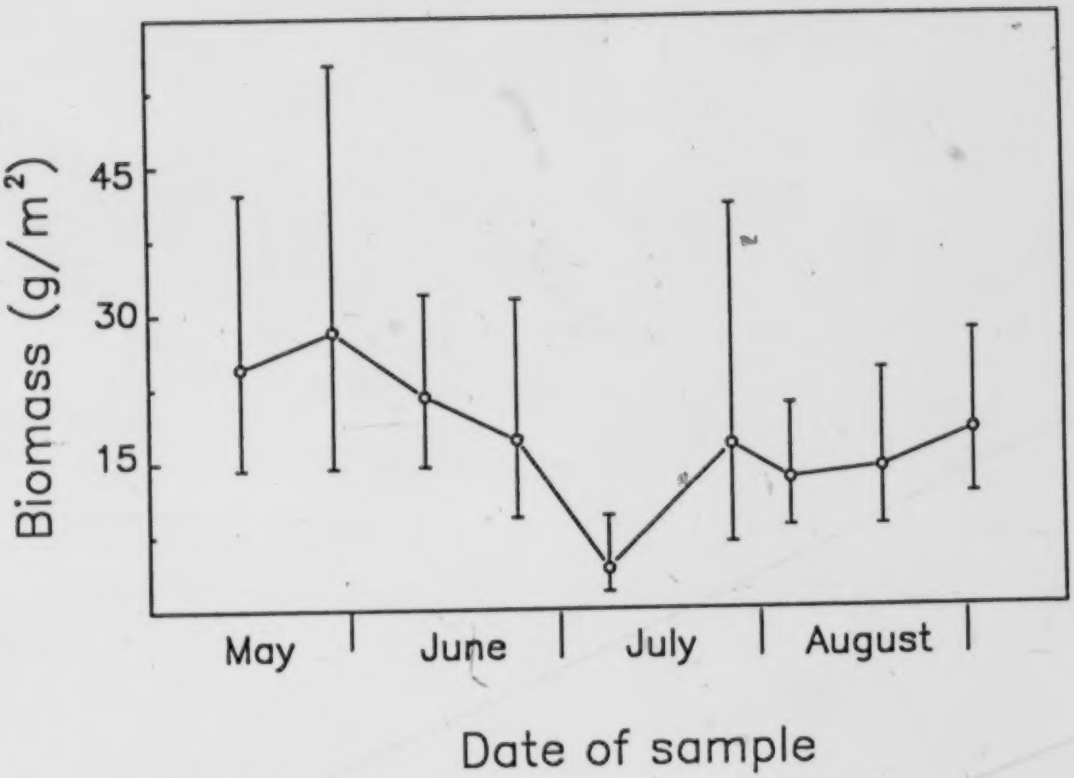

Figure 4.6. Average total benthic invertebrate biomass at the 1 m depth during the summer of 1986 in Narrow Lake. Vertical bars indicate 95% C.I.

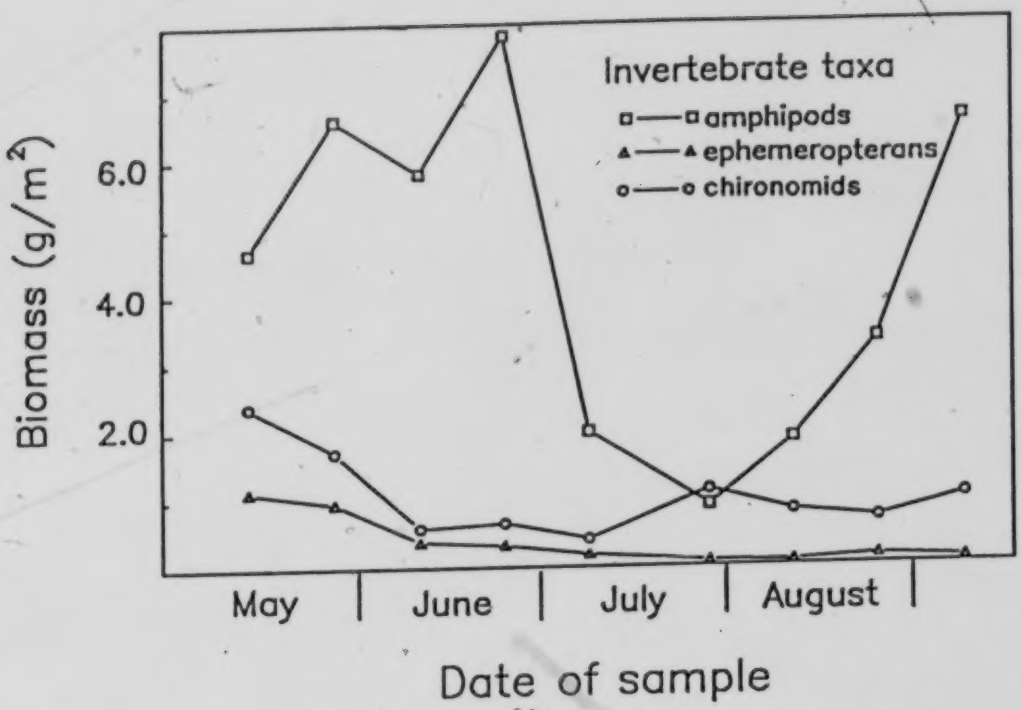

Figure 4.7. Change in biomass of major benthic invertebrates at the 1 m depth during the summer of 1986 in Narrow Lake.

perch. Although the biomass of these invertebrates increased again by the beginning of September (Figure 4.7), amphipods did not contribute more than 10% (by weight) to stomach contents of the perch at the end of the summer (Figure 4.3).

Figure 4.8 shows the proportions of amphipods in the lake and in perch stomachs. A larger proportion of a prey item in the stomach contents as compared to prey taxa as a proportion of total benthic biomass may indicate that the fish selectively feed on that prey taxon. More amphipods were eaten in June by the larger size class of perch when biomass of amphipods was greatest. However, an increase in the amount of amphipods eaten by the perch in August did not accompany the increase in biomass of amphipods in August.

1986 Experiments

Perch stomach contents

Prey items found in the stomachs of the perch held in the enclosures consisted mainly of amphipods and microcrustaceans (Figure 4.9). Microcrustaceans (cladocerans and copepods) were the dominant prey items in the stomachs of perch held in the enclosures both in terms of frequency of occurrence and by weight (Table 4.3). At the end of the first experiment, the food of perch in the enclosures included invertebrates such as hydracarinids, corixids, copepods, and gastropods, which were not found in the stomachs of perch living under natural conditions in Narrow Lake (Figure 4.9). Perch in the lake ate exclusively cladocerans and chironomids (Table 4.3). Invertebrates in the rare prey category were important in the diets in the second experiment.

Amphipods contributed more on a weight basis to the stomach contents of the perch in the lower density enclosures in both experiments than in the high density enclosures (Figure 4.9). The opposite trend was observed for the contributions of microcrustaceans to the stomach contents (Figure 4.9). The proportion of microinvertebrates eaten was less for perch held in the enclosures than for those in the lake (Figure 4.10). At the end of the first experiment, perch in the high density enclosure had eaten a greater proportion of microinvertebrates than perch in the other enclosure (ANOVA $P<0.001$, Appendix 3 Table

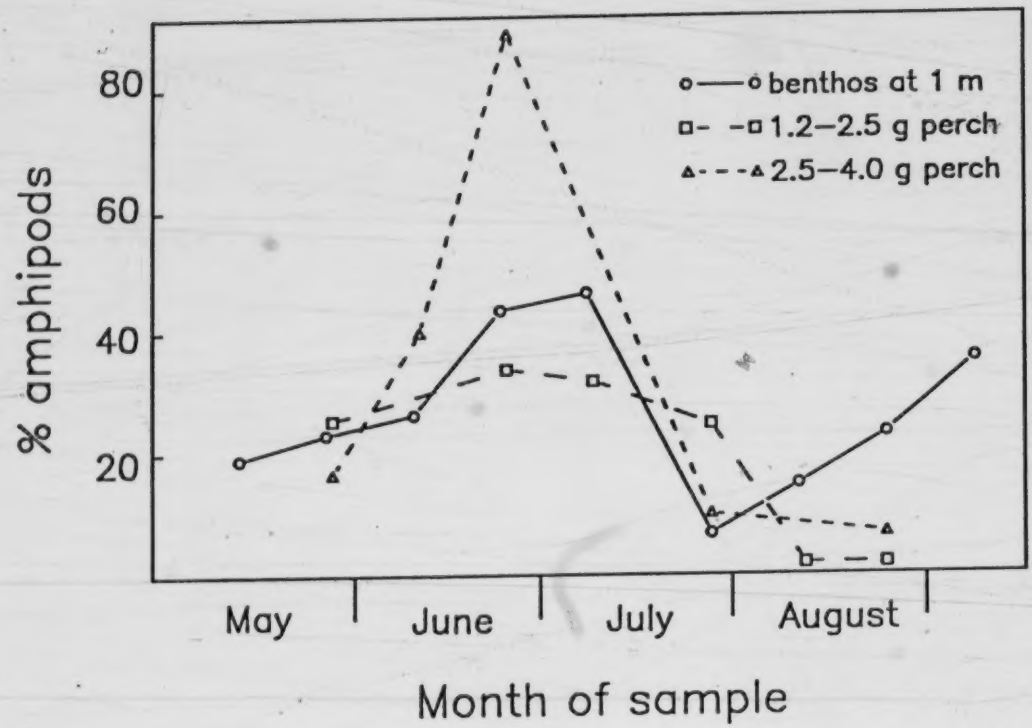

Figure 4.8. Amphipods as a % by weight [(mg amphipods/mg total stomach contents)*100] in the diets of small (1.20-2.50 g) and large (2.51-4.00 g) perch and as a % of total benthic biomass at the 1 m depth in Narrow Lake during May-August, 1986.

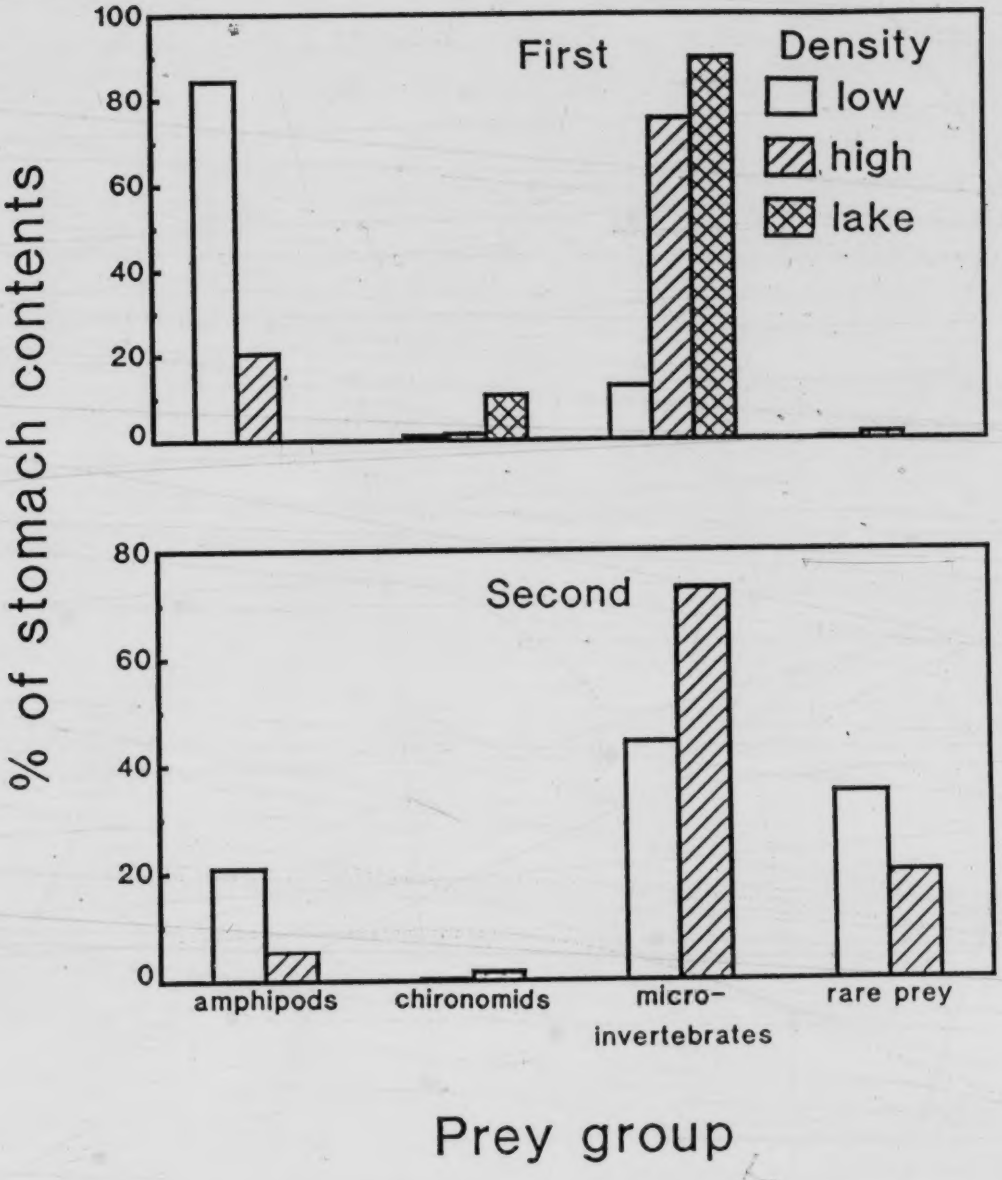

Figure 4.9. Stomach contents (% by weight) of perch in enclosures at low and high perch densities (6.8-10.4 g/m²) and in the lake (2.6 g/m²) in 1986. Rare prey taxa include ephemeropterans, trichopterans, corixids, ceratopogonids and coleopterans. First experiment was from July 15 to August 11 and the second experiment was from August 18 to September 9, 1986. Perch from the lake were collected on Aug. 19, 1986.

TABLE 4.3. Stomach contents (% by weight and frequency of occurrence) of perch in enclosures at low and high densities in experiments testing for intraspecific competition in 1986. Perch used in the experiments were between 1.5 and 3.1 g (weight ± SD = 2.34 ± 0.36 g). Rare prey items included corixids, trichopterans, coleopterans, gastropods, and ceratopogonids. Perch were collected from the lake on August 19, 1986.

	Perch density					
	Low		High		Lake Density 2.6 g/m²	
Prey type	% weight	freq.	% weight	freq.	% weight	freq.
	FIRST EXPERIMENT: Stocking date July 15, Recovery date Aug. 12					
	7.4 g/m²		10.4 g/m²			
Amphipods	84.3	37.2	20.4	13.7	0	0
Chironomids	1.0	14.0	1.4	11.8	10.5	20.0
Ephemeropterans	0.3	4.7	0.4	2.0	0	0
rare prey	0	0	1.1	7.8	0	0
Microcrustaceans	10.3	25.6	68.4	43.1	89.5	80.0
Hydracarinids	2.2	18.6	6.9	21.6	0	0
unidentified	1.9		1.4	0	0	0
	SECOND EXPERIMENT: Stocking date Aug. 18, Recovery date Sept. 9					
	6.8 g/m²		10.3 g/m²			
Amphipods	20.8	12.5	5.5	13.6		
Chironomids	0.3	3.6	1.6	4.5		
Ephemeropterans	24.3	33.2	2.1	4.5		
rare prey	10.4	7.1	17.8	13.6		
Microcrustaceans	44.2	53.5	67.4	56.8		
Hydracarinids	0	0	5.6	6.8		
unidentified	0		0			

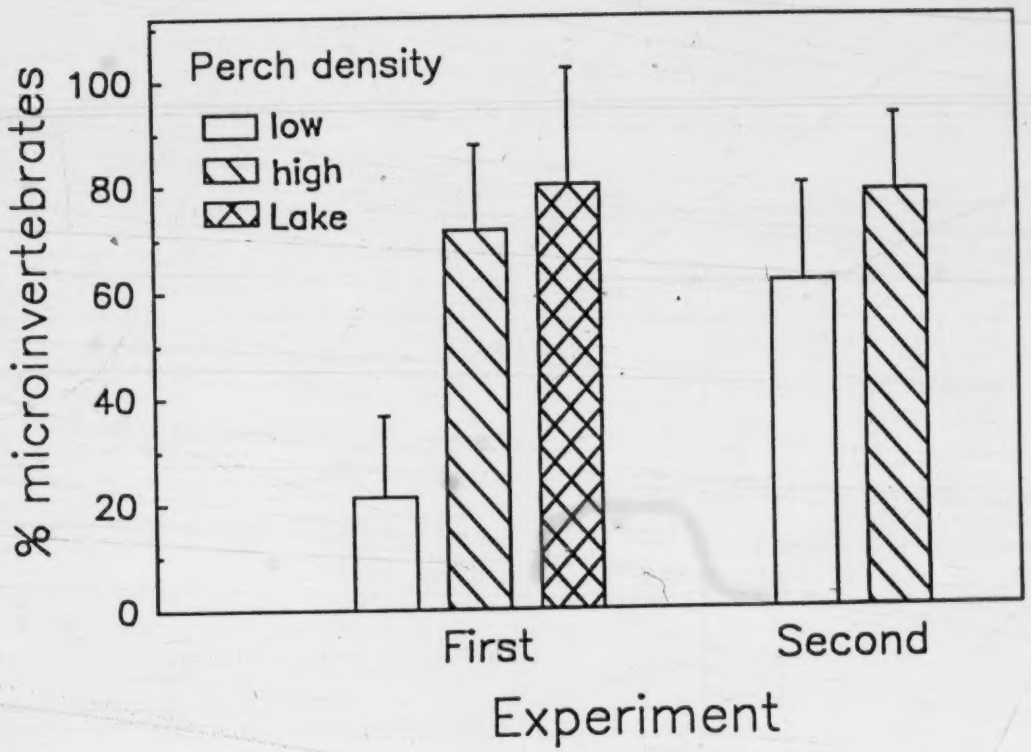

Figure 4.10. Proportion of microinvertebrates [(mg microinvertebrates/mg total stomach contents)*100] in the diets of perch in enclosures at low and high perch densities (6.8-10.4 g/m²) in 1986. Perch from the lake (2.6 g/m²) were caught on Aug. 19, 1986. The first experiment was from July 15 to August 11 and the second was from August 18 to September 9, 1986. Means and 95% C.I. (vertical bars) of perch in each enclosure are given.

2). In the second experiment ending September 9, no difference in the proportion of microinvertebrates eaten by the perch was observed between densities (ANOVA P=0.3). The proportion of microinvertebrates in the stomachs was greater than 60% for perch in both the high and low density enclosures in the second experiment.

Stomach fullness of the perch differed between enclosures in the first experiment (Figure 4.11; ANOVA P<0.001) Mean stomach fullness of perch held in the high density enclosure was significantly less than that of perch held at low density (SNK) and the perch in the lake on August 6 (SNK). In the second experiment, stomach fullness of the perch was not different between treatments (Figure 4.11).

Benthic community

The benthic community in the enclosures in 1986 was composed of 14 taxa (Table 4.4) of which one taxon, Amphipoda, was eaten regularly and six taxa which were eaten rarely by perch. Amphipods were the most abundant invertebrates (>70% by weight and by number) in the enclosures immediately preceeding the experiments on July 11, 1986. Since the total biomass within the enclosures was different at the start of the experiment, the benthic communities within the enclosures were analysed separately.

Biomass and abundance of benthic invertebrates eaten by perch decreased during the first experiment and increased during the second, except for amphipods and trichopterans, in the low density enclosures (Table 4.4). The proportion of prey taxa eaten by perch as a % of total benthic biomass in the enclosures decreased from 85% to 63% in the first experiment to 47% by the end of the second experiment. The biomass of amphipods decreased significantly over the first experiment (Student's t-test P<0.001) but not during the second (Student's t-test P=0.99)(Figure 4.12). The biomass of invertebrates eaten only rarely by the perch did not change during the experiments (ANOVA P=0.16). Total benthic biomass in the enclosure decreased significantly over the first experiment (Student's t-test P<0.01) but not during the second experiment (Student's t-test P=0.3)(Figure 4.12). Total benthic biomass at the 1 m

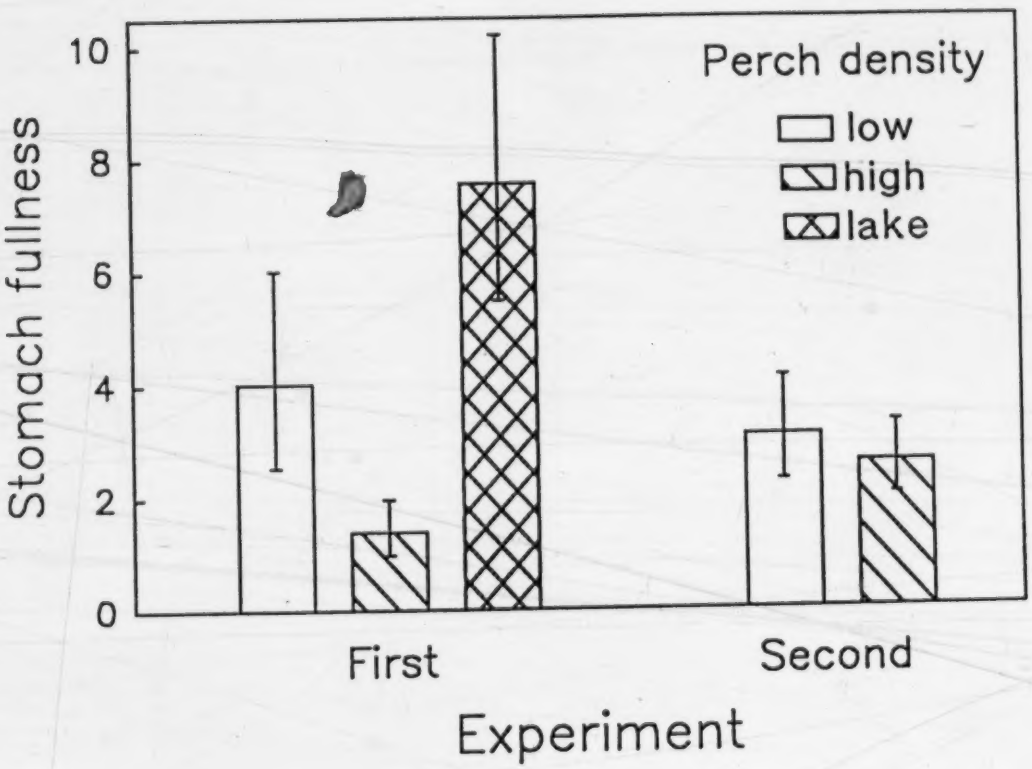

Figure 4.11. Stomach fullness (mg food/g fish) of perch in enclosures at low and high perch densities (6.8-10.4 g/m²) in 1986 to test the effect of perch density on diet. Perch from the lake (2.6 g/m²) were caught on Aug. 19, 1986. The first experiment was from July 15 to August 11 and the second experiment was from August 18 to September 9, 1986. Means and 95% C.I. (vertical bars) of perch in each enclosure are given.

TABLE 4.4. Benthic invertebrate community in enclosures held at low and high perch densities in two experiments in 1986 testing for evidence of intraspecific competition.

Taxa	Date of sample: July 11 Biomass g/m²	% of total biomass	No./ m²	Aug. 12 Biomass g/m²	% of total biomass	No./ m²	Sept. 9 Biomass g/m²	% of total biomass	No./ m²
				Low perch density (6.8-7.4 g/m²)					
Amphipoda	21.00	70.0	19431	1.80	25.8	2693	1.79	20.6	1093
Chironomidae	2.32	7.7	5147	0.59	8.4	1751	1.81	20.9	8444
Ephemeroptera	0.29	1.0	293	0.02	0.3	71	0.91	2.2	356
Ceratopogonidae	0.08	0.3	116	0.02	0.3	18	0.05	0.6	36
Trichoptera	1.61	5.4	133	1.92	27.5	53	0.06	0.7	116
Coleoptera	0.01	0.0	18	0.0	0.0	18	0.00	0.0	0
Gastropoda	0.53	1.8	258	1.10	15.7	382	2.18	25.1	284
Hirudinea	0.39	1.3	44	0.04	0.6	36	0.04	0.4	36
Turbellaria	1.88	6.3	320	0.13	1.9	124	0.37	4.3	267
Oligochaeta	0.16	0.5	338	0.20	2.9	836	0.82	9.4	2702
Sphaeriidae	0.84	2.8	507	0.87	12.4	596	0.96	11.1	720
Anisoptera	0.87	2.9	62	0.26	3.7	27	0.11	1.3	27
Chrysomelidae	0.00	0.0	0	0.04	0.6	18	0.30	3.5	53
Nematomorpha	0.01	0.0	53	0.00	0.0	9	0.00	0.0	0
TOTAL	30.00			6.99			8.67		
				High perch density (10.3 -10.4 g/m²)					
Amphipoda	11.36	73.0	7911	1.23	35.0	1511	0.63	12.9	311
Chironomidae	1.13	7.3	1644	0.39	11.1	1671	1.54	31.5	5467
Ephemeroptera	0.26	1.7	293	0.02	0.6	62	0.04	0.8	98
Ceratopogonidae	0.01	0.1	18	0.06	1.7	80	0.06	1.2	89
Trichoptera	1.00	6.4	53	0.25	7.1	27	0.03	0.6	62
Gastropoda	1.13	7.3	267	0.71	20.3	231	0.79	16.1	471
Hirudinea	0.16	1.0	71	0.02	0.7	27	0.05	1.0	27
Turbellaria	0.03	0.2	9	0.19	5.1	80	0.23	4.7	98
Oligochaeta	0.08	0.5	89	0.15	4.4	311	0.48	9.8	1324
Sphaeriidae	0.40	2.6	267	0.07	2.0	116	0.41	8.3	676
Anisoptera	0.00	0.0	0	0.28	8.0	18	0.33	6.7	18
Chrysomelidae	0.00	0.0	0	0.14	4.0	27	0.31	6.3	44
Nematomorpha	0.01	0.1	62	0.00	0.0	0	0.00	0.0	9
TOTAL	15.57			3.51			4.89		

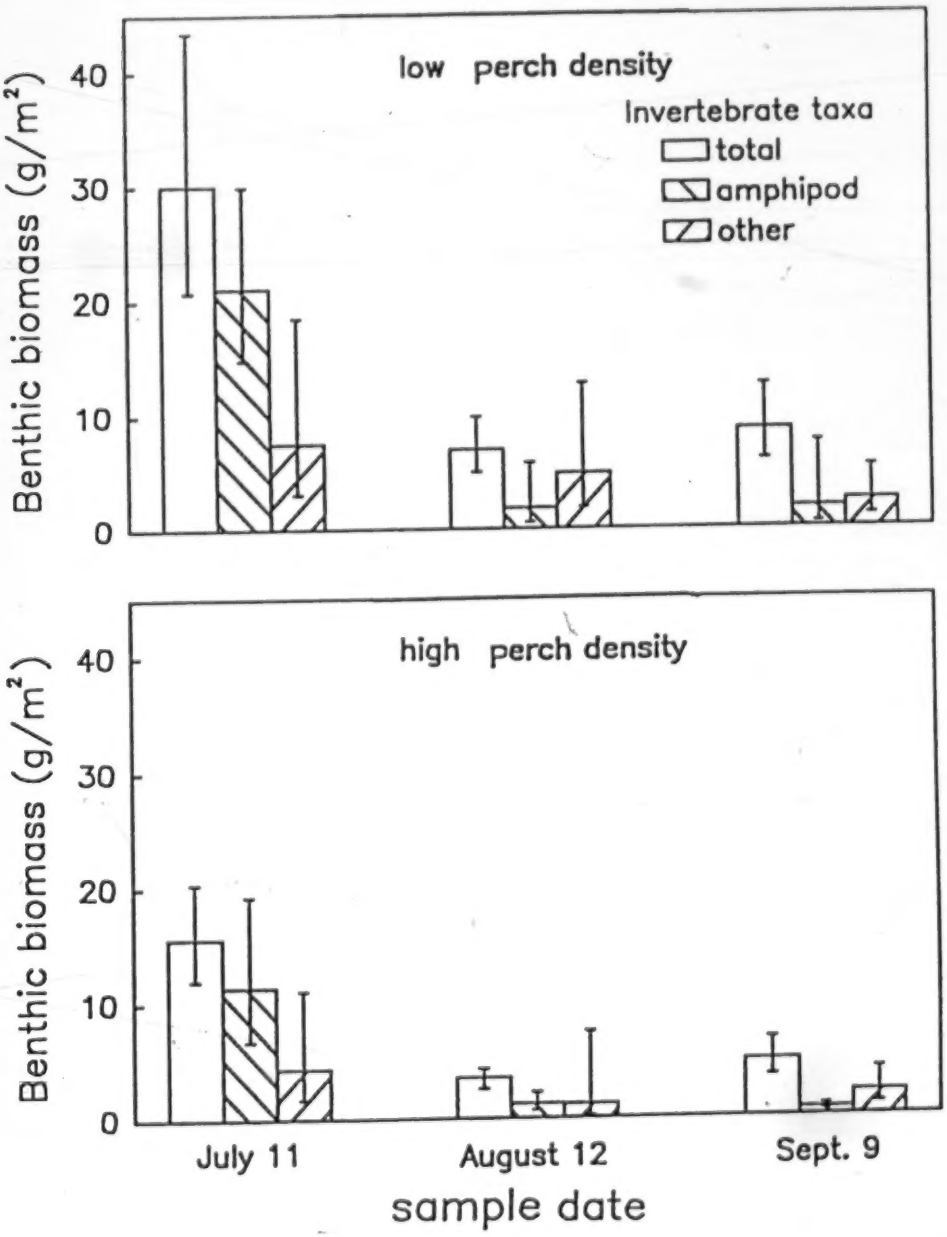

Figure 4.12. Average biomass of macroinvertebrates in enclosures at low and high perch densities (6.8-10.4 g/m²) in 1986. Benthos was sampled within a few days of the stocking (July 15 and August 12) and removing (August 18 and September 9) perch in the two experiments. Other invertebrates includes all types of benthic invertebrates eaten by perch except amphipods. Means and 95% C.I. (vertical bars) are presented.

depth in the littoral zone of the lake increased from 4.7 g/m² on July 22, 1986, to >13 g/m² throughout August and the beginning of September, 1986.

In the high density enclosure, the abundance and biomass of amphipods decreased throughout the experiments whereas other prey types showed no change or increased in biomass (Table 4.4). The proportion of prey types eaten by perch as a % of total benthic biomass in the enclosure decreased from 89% to 49% by the end of the experiments. The biomass of amphipods decreased significantly over both experiments (ANOVA $P<0.01$)(Figure 4.12). The biomass of invertebrates eaten rarely did not change during the experiments (ANOVA $P=0.28$). Total benthic biomass decreased significantly within the enclosure during the first experiment (Student's t-test $P<0.001$) but not the second (Student's t-test $P=0.2$).

1987 Experiments

Perch stomach contents

Stomach contents of perch in the enclosures in 1987 is shown in Figure 4.13. At the end of the June 1987 experiment, the dominant prey item by weight and frequency of occurrence of perch in the enclosures and the lake was amphipods (Table 4.5). The majority of prey items eaten by perch in the enclosures were macroinvertebrates (>97% by weight, 92% by frequency of occurrence)(Table 4.5). The proportion of microinvertebrates in the stomachs of the perch in the lake in June was 30% whereas the perch in the enclosures ate significantly fewer (<4%) microinvertebrates (Appendix 3 Table 2). Stomach fullness varied significantly between the treatments and the lake (Figure 4.14; ANOVA $P=0.01$). Stomach fullness was greater for perch held in the medium and high density enclosures than for the perch caught in the lake at the same time (SNK).

The diets of the perch in the enclosure experiments conducted in July and August were similar (Table 4.5) although more microinvertebrates were eaten at the end of the August experiment (Figure 4.15). In the two experiments, the amount of amphipods in the stomachs (% by weight) was inversely related to perch density in the enclosures and the amount of

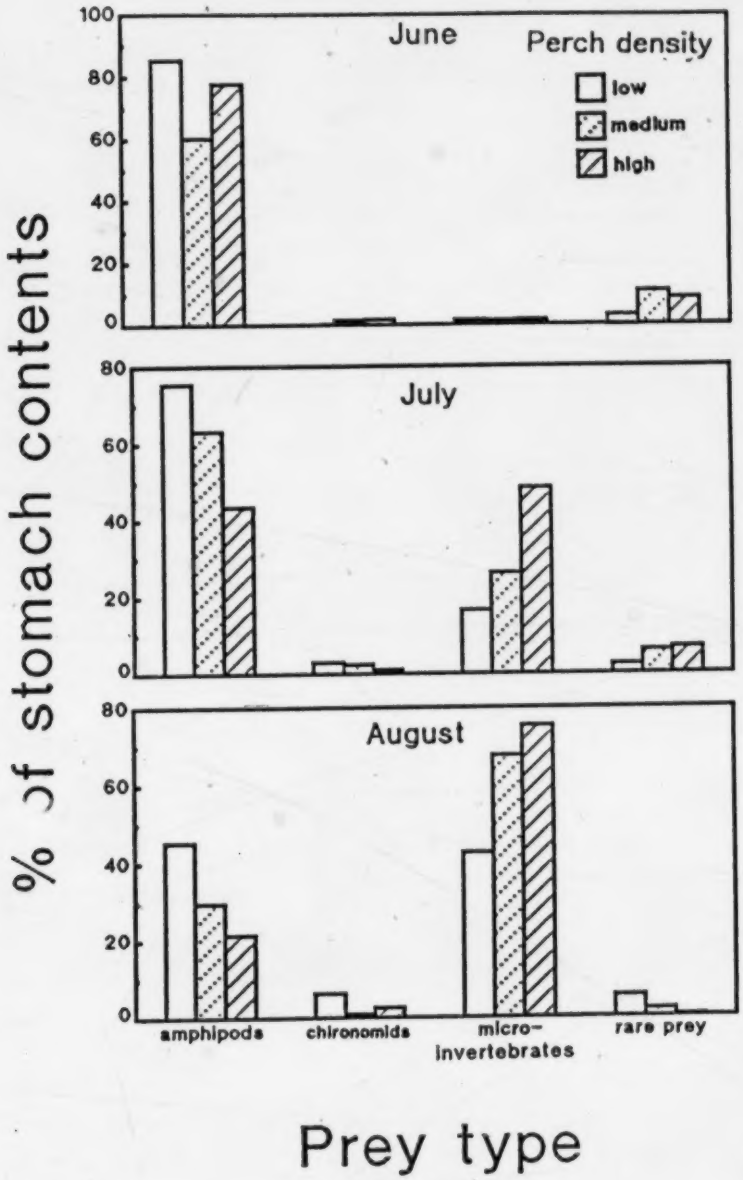

Figure 4.13. Stomach contents (% by weight) of perch in enclosures at various perch densities (1.7-7.0 g/m²) in 1987. Rare prey taxa include ephemeropterans, trichopterans, corixids, ceratopogonids and coleopterans. (Refer to Table 3.2 for exact perch densities).

TABLE 4.5. Stomach contents (% by weight and frequency of occurrence) of perch in enclosures at various densities in three experiments in 1987. Perch used in the experiments were between 1.5 and 3.1 g. Rare prey items included corixids, trichopterans, coleopterans, gastropods, ephemeropterans (except for the June experiment), and ceratopogonids.

Prey type	Perch density: Low % weight	Low freq.	Medium % weight	Medium freq.	High % weight	High freq.	Lake Density % weight	Lake Density freq.
	JUNE EXPERIMENT: Stocking date June 11, Recovery date July 1							
	1.8 g/m²		3.5 g/m²		5.0 g/m²		1.1 g/m²	
Amphipods	86.2	48.8	62.8	37.5	77.6	37.0	63.9	40.4
Chironomids	0.3	4.7	1.0	8.9	1.7	11.1	0	0
Ephemeropterans	8.3	25.6	20.8	23.2	9.3	22.2	2.1	17.0
rare prey	3.5	16.3	12.1	23.2	10.0	22.2	7.3	25.5
Microcrustaceans	1.6	4.7	3.0	7.1	1.5	7.4	15.7	12.8
unidentified							11.0	4.3
	JULY EXPERIMENT: Stocking date July 8, Recovery date July 29							
	3.6 g/m²		6.0 g/m²		7.0 g/m²		1.1 g/m²	
Amphipods	75.5	31.1	63.3	34.8	43.6	26.9	35.4	33.3
Chironomids	3.0	20.0	2.4	17.4	1.1	7.7	6.8	22.8
rare prey	2.3	24.4	6.0	17.4	6.8	11.5	1.8	7.0
Microcrustaceans	15.0	20.0	22.1	26.1	45.9	44.3	35.4	31.6
Hydracarinids	1.5	4.4	4.1	4.3	2.6	9.6	0	
unidentified†	2.7		2.0				20.6	5.3

TABLE 4.5. Continued. Stomach contents (% by weight and frequency of occurrence) of perch in enclosures at various densities in three experiments in 1987. Perch used in the experiments were between 1.5 and 3.1 g. Rare prey items included corixids, trichopterans, coleopterans, gastropods, ephemeropterans (except for the June experiment), and ceratopogonids.

Prey type	Perch density: Low % weight	Low freq.	Medium % weight	Medium freq.	High % weight	High freq.	Lake Density % weight	Lake Density freq.
	AUGUST EXPERIMENT: Stocking date August 3, Recovery date August 24							
	3.8 g/m²		4.1 g/m²		6.6 g/m²		1.4 g/m²	
Amphipods	29.6	15.6	45.4	28.1	21.6	15.8	27.3	26.8
Chironomids	0.9	9.4	6.3	18.7	2.6	5.3	8.9	22.0
rare prey	2.0	9.4	5.6	9.4	0.4	5.3	0.6	4.9
Microcrustaceans	52.6	56.2	42.7	43.7	75.3	73.6	56.5	41.5
unidentified††	14.9	9.4					6.7	4.9

†includes fish in stomachs of perch caught in the lake
††includes chaoborids in stomachs of perch caught in the lake

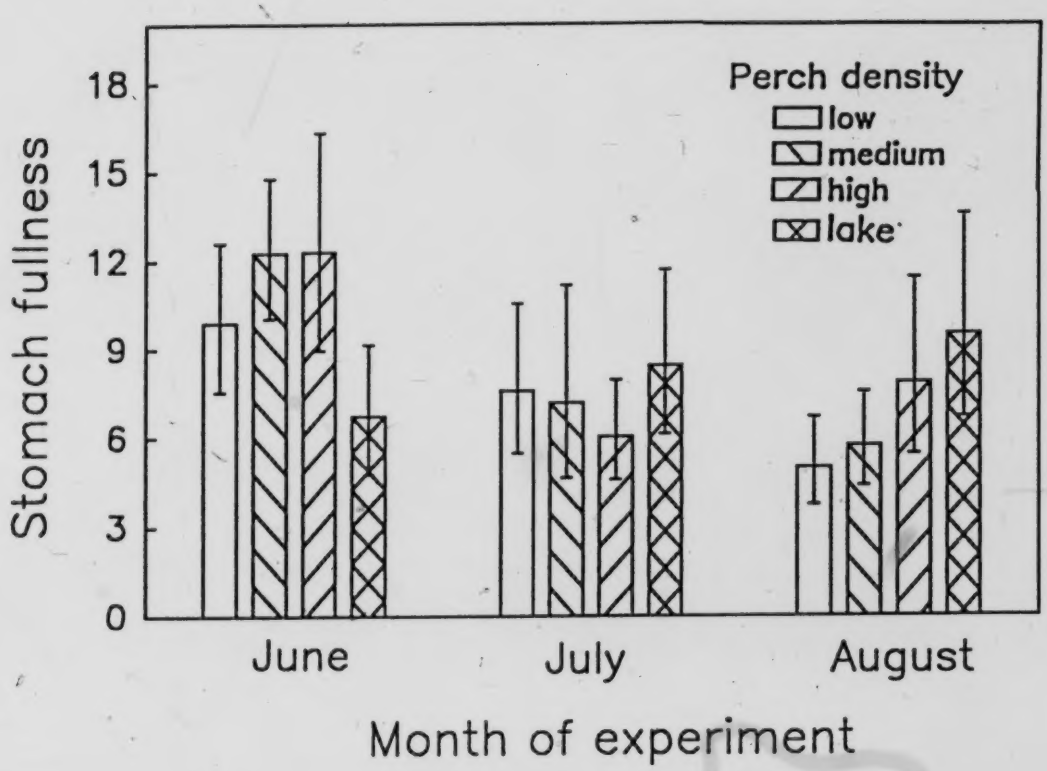

Figure 4.14. Stomach fullness (mg food/g fish) of perch in enclosures at various perch densities (1.7-7.0 g/m²) in 1987 experiments testing the effect of perch density on diet. Perch from the lake (1.1-1.4 g/m²) were caught on the days each experiment was ended. Means and 95% C.I. (vertical bars) of perch in each enclosure are given. (Perch in enclosures receiving duplicate treatments were pooled). Refer to Table 3.2 for exact densities.

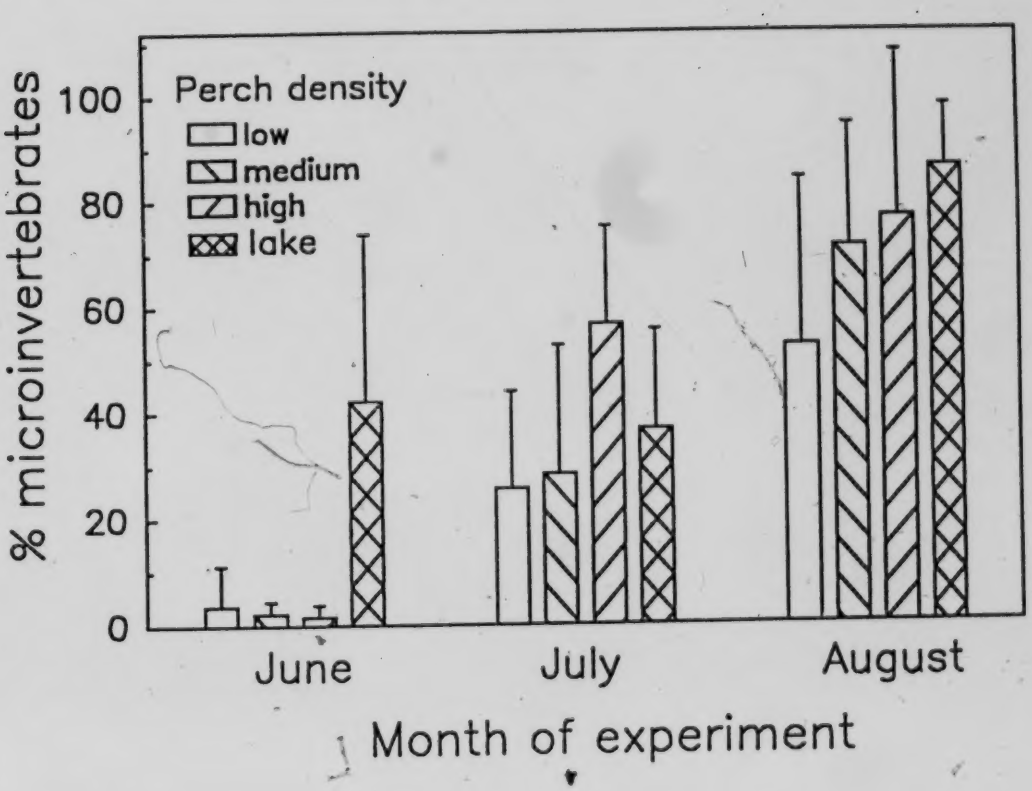

Figure 4.15. Proportion of microinvertebrates [(mg microinvertebrates/mg total stomach contents)*100] in the diets of perch in enclosures at various perch densities (1.7-7.0 g/m²) in 1987. Perch from the lake (1.1-1.4 g/m²) were caught on the days each experiment was ended. Means and 95% C.I. (vertical bars) of perch in each enclosure are given (perch in enclosures receiving duplicate treatments were pooled). Refer to Table 3.2 for exact densities.

microinvertebrates eaten (% by weight) was positively related to perch density (Figure 4.13). The perch ate a greater proportion of microinvertebrates at the end of the experiment in August than in July (ANOVA $P=0.01$). Perch living under natural conditions in the lake had significantly more microinvertebrates in their stomachs in August than in July also (ANOVA $P=0.01$). However, no difference was observed in the amount of microinvertebrates eaten by the perch at different densities and perch in the lake within each experiment (ANOVA both $P>0.10$; Figure 4.15) nor in the fullness of the stomachs for both experiments (ANOVA $P=0.09$; Figure 4.14)

Benthic community

The benthic community in the enclosures of the June 1987 experiment was composed of 13 taxa (Table 4.6). The most abundant invertebrates were amphipods (56-78% by weight) and trichopterans (7-27% by weight) immediately preceeding the experiment. Amphipods were by far most abundant by number/m^2. Total benthic biomass and biomass of invertebrates eaten by perch did not differ between enclosures at the start of the experiment (ANOVAs all $P>0.22$).

The total biomass of benthic invertebrates decreased between the beginning and end of the June experiment in all enclosures (Table 4.6). However, the total biomass of benthic invertebrates at the end of the experiment did not vary with perch density (ANOVA $P=0.3$). Biomass of prey taxa eaten by perch did not vary either (ANOVAs all $P>0.11$). Perch density did not affect the biomass of benthic invertebrates within the enclosures in June. The similar changes in benthic invertebrate biomass within all enclosures, including the zero perch density enclosure, over the experiments would be the result of natural variation in the invertebrate community over time.

TABLE 4.6. Benthic invertebrate community in enclosures held at various perch densities in the experiment in June, 1987, testing for evidence of intraspecific competition. Data given are average fresh weights (backcalculated) of five grabs per enclosure at the start and end of the experiment. Data from replicate treatments were combined.

	Date of sample					
	June 9			July 1		
Taxa	Biomass g/m²	% of total biomass	No./ m²	Biomass g/m²	% of total biomass	No./ m²
	Enclosure perch density = 1.8 g/m²					
Amphipoda	16.24	78.1	2778	9.16	78.6	5044
Chironomidae	1.46	7.0	1213	0.79	6.8	1396
Ephemeroptera	0.06	0.3	36	0.05	0.4	80
Ceratopogonidae	0.23	1.1	71	0.06	0.5	89
Trichoptera	1.50	7.2	284	0.49	4.2	213
Gastropoda	0.77	3.7	133	0.38	3.2	160
Hirudinea	0.18	0.9	31	0.38	3.3	24
Turbellaria	0.07	0.3	31	0.22	1.9	62
Oligochaeta	0.13	0.6	36	0.03	0.2	44
Sphaeriidae	0.13	0.6	169	0.04	0.34	80
Anisoptera	0.00	0.0	0	0.00	0.0	4
Chrysomelidae	0.00	0.0	4	0.01	0.0	22
Nematomorpha	0.03	0.1	111	0.07	0.6	76
TOTAL	20.80			11.66		
	Enclosure perch density = 3.5 g/m²					
Amphipoda	11.02	55.8	2427	3.94	62.4	2922
Chironomidae	1.27	6.4	1173	1.07	16.9	1344
Ephemeroptera	0.09	0.4	53	0.08	1.3	67
Ceratopogonidae	0.12	0.6	11	0.01	0.2	67
Trichoptera	5.43	27.5	364	0.22	3.5	133
Gastropoda	0.29	1.5	89	0.16	2.53	44
Hirudinea	0.65	3.3	27	0.03	0.5	67
Turbellaria	0.04	0.2	18	0.13	2.1	33
Oligochaeta	0.66	3.3	276	0.60	9.5	144
Sphaeriidae	0.06	0.3	44	0.05	0.9	78
Anisoptera	0.08	0.4	9	0.00	0.0	0
Chrysomelidae	0.01	0.0	44	0.00	0.0	0
Nematomorpha	0.03	0.2	53	0.02	0.3	22
TOTAL	19.75			6.31		

TABLE 4.6. Continued. Benthic invertebrate community in enclosures held at various perch densities in the experiment conducted in June, 1987, testing for evidence of intraspecific competition. Data given are average fresh weights (backcalculated) of five grabs per enclosure at the start and end of the experiment. Data from replicate treatments were combined.

	Date of sample					
	June 9			July 1		
Taxa	Biomass g/m²	% of total biomass	No./ m²	Biomass g/m²	% of total biomass	No./ m²
	Enclosure perch density = 5.0 g/m²					
Amphipoda	14.14	68.7	2613	7.94	77.4	8142
Chironomidae	1.84	9.0	1991	1.17	11.4	1529
Ephemeroptera	0.12	0.6	80	0.04	0.4	36
Ceratopogonidae	0.08	0.4	142	0.12	1.1	133
Trichoptera	2.09	10.1	320	0.12	1.2	222
Gastropoda	0.37	1.8	142	0.11	1.1	89
Hirudinea	0.72	3.5	71	0.06	0.6	44
Turbellaria	0.13	0.6	36	0.09	0.9	18
Oligochaeta	0.04	0.2	89	0.01	0.0	27
Sphaeriidae	0.89	4.3	133	0.24	2.34	187
Anisoptera	0.09	0.4	18	0.00	0.0	9
Chrysomelidae	0.00	0.0	9	0.08	0.8	1
Nematomorpha	0.08	0.4	178	0.28	2.7	258
TOTAL	20.58			10.26		
	Enclosure perch density = 0 g/m²					
Amphipoda	16.00	72.3	2604	8.01	82.3	5358
Chironomidae	1.32	6.0	809	0.61	6.39	6374
Ephemeroptera	0.07	0.3	40	0.19	1.9	153
Ceratopogonidae	0.14	0.6	240	0.51	0.5	148
Trichoptera	2.83	12.8	151	0.21	2.2	227
Gastropoda	0.73	3.3	147	0.20	2.13	104
Hirudinea	0.65	2.9	67	0.22	2.2	119
Turbellaria	0.12	0.5	36	0.02	0.2	10
Oligochaeta	0.06	0.3	53	0.07	0.7	79
Sphaeriidae	0.17	0.8	222	0.08	0.9	143
Chrysomelidae	0.00	0.0	9	0.00	0.0	15
Nematomorpha	0.03	0.1	107	0.08	0.8	69
TOTAL	22.12			9.73		

D. DISCUSSION

Intraspecific competition

At high levels of intraspecific competition, the amount of food eaten by perch (<3.5 g) in the enclosures was significantly reduced (Figure 4.11). Perch ate approximately five times as much food under natural conditions in the lake as they did at a density three times the biomass of fish in the littoral zone. Perch held at a density three times the natural biomass ate approximately one third the amount of food compared to perch in the lake (in 1986). Hanson and Leggett (1986) also found the amount of food eaten by perch (5-35 g body weight) in enclosures stocked at a density twice the natural fish biomass in the littoral zone of Lake Memphremagog, Quebec, was significantly less than perch reared at natural density (13 g/m^2). The mean ration size of yearling largemouth and spotted bass in monotypic ponds in Oklahoma was significantly larger in ponds stocked at low density than in high density ponds (Clady and Luker 1982). These results support the hypothesis that increasing levels of competition cause a decrease in the quantity of food eaten by individuals (Hanson and Leggett 1986, Mittelbach 1988).

More microinvertebrates were eaten by perch at high perch densities than at low densities, indicating higher levels of competition for macroinvertebrates within the enclosures. Hanson and Leggett (1986) proposed that increasing levels of competition would result in the fish including inferior prey items, such as microcrustaceans, in their diets. They found that perch reared with pumpkinseed sunfish had a diet composed of 30-53% microcrustaceans (by weight) whereas the diet of perch reared alone at the same density contained less than 1% microcrustaceans. Increased competition can decrease prey resource variation, since fish can decrease the abundance of large macroinvertebrates (Post and Cucin 1984, Persson 1986, Mittelbach 1988). Therefore, the fish include more abundant prey items in their diets, such as zooplankton, when preferred prey are less available, and they will increase the size range of prey eaten.

Fish can increase the range of prey types eaten when prey resource abundance is decreased. Perch in the high density enclosures in Narrow Lake included prey types (corixids, leeches, copepods, and hydracarinids) in their diets that were not found in the stomachs of perch under natural conditions in the lake. Clady and Luker (1982) found a greater frequency of selection for rarely eaten invertebrates in high density ponds than in low density ponds.

At high perch densities ($\geq$6.8 g/m^2), the biomass of amphipods decreased within the enclosures, whereas in the lake the biomass of amphipods increased. Unfortunately, because no replication of treatments could be done in 1986 other than over time, an inverse relationship between perch density and density of benthic invertebrates could not be demonstrated. However, there was a significant change in abundance of amphipods over time within the enclosures compared to the littoral zone, indicating that competition for amphipods was occurring at high perch densities. Such an alteration of the food resource in response to competition was predicted by Mittelbach (1988). In turn, the decrease in abundance of the food resource would lead to a shift in diet from amphipods to other prey types such as observed in the enclosures. Persson (1986) also observed a shift in prey types consumed by perch following a decrease in abundance of preferred invertebrate groups.

Perch densities from zero to three times the measured natural fish biomass in the littoral zone did not result in changes in total benthic biomass or biomass of invertebrates regularly eaten by perch in the experiment in June. In this experiment, perch density did not affect stomach fullness, nor the proportion of microinvertebrates eaten. Therefore, the finding of no change in total benthic biomass at different perch densities was consistent with the other findings that perch density did not affect the amount of food eaten or the proportion of microinvertebrates eaten in the June experiment. In June, the perch may not be competing for macroinvertebrates. Or, at lower levels of competition, a change in food biomass may not be detectable (Hanson and Leggett 1986). Boisclair and Leggett (1985) found that daily food consumption by fish in the littoral zone of Lake Memphremagog was <1% of invertebrate biomass. Responses of the benthic community to fish predation have

been observed in some studies (Crowder and Cooper 1982, Post and Cucin 1984) but not in others (Hall *et al.* 1970, Hanson and Leggett 1986).

At lower perch densities (1 to 2.5 times the natural lake biomass), no significant differences were observed in mean stomach fullness or in the relative importance of microinvertebrates in the diets between perch from the enclosures and the lake. The absence of an effect at these densities is probably the result of natural variation in perch feeding habits. Perch are opportunistic feeders, the diet being determined by prey availability, size, habitat structure, foraging efficiency and other such factors (Keast 1977, Werner and Hall 1976, Persson 1987b).

This study showed that at high perch density the amount of food eaten and the type of prey eaten by perch changes compared to the diet of perch at lower densities. Intraspecific competition leads to perch including in their diets smaller prey items (microinvertebrates) and other prey types not usually eaten and leads to a decrease in the quantity of food eaten. High levels of competition also resulted in a decrease in biomass of invertebrate prey groups within the enclosures. Competition between perch within one size category can have a significant effect on the quality and quantity of the diet.

Diet of perch in Narrow Lake

Feeding activity of the perch <4.0 g and 85 mm in Narrow Lake was maximum in early morning both in July and August. Perch in Lake Memphremagog, Quebec, fed most actively in the early morning in July and August (Hanson and Leggett 1985). Other studies have described peaks in feeding intensity as changing from dawn and dusk activity in spring (May and June) to a mid-day activity peak in late August (Nakashima and Leggett 1978, Persson 1983a, Rask 1986).

Changes in the diet of perch <4.0 g in Narrow Lake appeared to coincide with changes in the abundance of potential prey items. For example, the dominance of chironomid pupae in the diet of the perch in May coincided with pre-emergence instars. Extensive use of chironomid pupae by perch in spring has been observed in other lakes (Keast 1977, Hayward

and Margraf 1987). The increase in importance of zooplankton in the diet toward the end of August, however, was not related to zooplankton abundance in the littoral zone of Narrow Lake. Zooplankton abundance did not change in the littoral zone in August (Figure 4.16).

The diet of the perch in Narrow Lake is comparable to that of other perch except that amphipods play a more important role in the diets of perch in Narrow Lake. The majority of the diet of perch (<4.0 g, 85 mm TL) in Narrow Lake was comprised of amphipods and cladocerans, although the smaller perch (1.21-2.50 g) ate slightly more cladocerans and fewer amphipods (by weight and frequency of occcurrence than larger perch (up to 4.0 g). Non-stunted perch of a comparable size (age 0+ <80 mm, age 1+ <120 mm) in other lakes eat mainly chironomids and cladocerans (Keast 1977, Nyberg 1979, Noble 1975, Nakashima and Leggett 1978). Stunted perch (age 1+ and 2+) in other lakes also ate predominantly cladocerans and chironomids (Eschmeyer 1937, Rask and Hiisivuori 1985).

In Narrow Lake, the diet differed between two size categories of perch less than 4.0 g and 85 mm TL. Differences in food selection between the two classes may be related to foraging efficiency and prey availability, as the diet differences disappeared in August. Then, the perch fed predominantly on zooplankton. Rask (1986) observed a similar diet shift for stunted perch over summer in Lake Horkkajärvi, Finland. Perch <110 mm (<4+) ate mainly cladocerans throughout summer, whereas perch 110-130 mm switched from benthic invertebrates in early summer to zooplankton by the end of summer (Rask 1986). The diet shift appeared to be related to an increase in zooplankton density to a maximum in September and a decrease in benthic biomass from May through June. Rask (1986) suggested that the decrease in benthic invertebrates was the result of increased predation pressure since perch can reduce the abundance of large macroinvertebrates such as trichopterans and anisopterans (Crowder and Cooper 1982, Post and Cucin 1984, Persson 1986, Mittelbach 1988). Age 1+ and 2+ perch in Lake Sövdeborg, Sweden, switched from macroinvertebrates in May and June to zooplankton in August through October when macroinvertebrate abundance decreased (Persson 1987b).

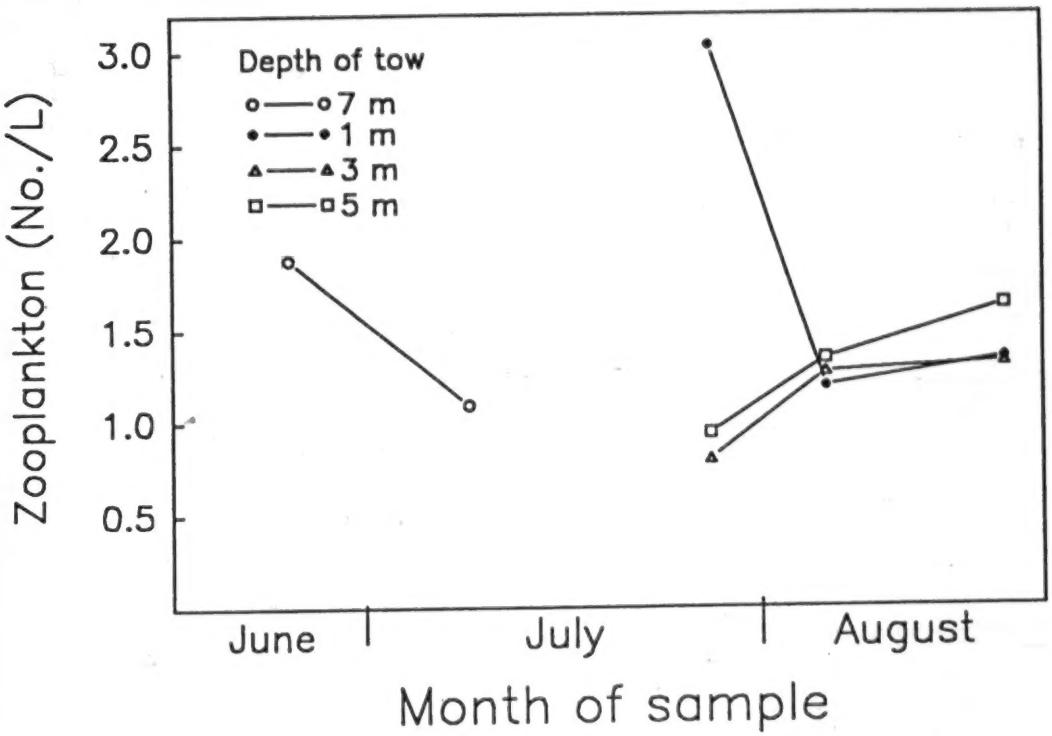

Figure 4.16. Zooplankton abundance (No./L) in the littoral zone of Narrow Lake during June-August, 1986 (D. Abbey, unpubl. data). Samples were collected using verticals tows (1-mm mesh plankton net).

In early summer, perch in these studies and in Narrow Lake fed on zooplankton and macroinvertebrates. Presumably the amount of each prey type eaten would depending on perch size, foraging efficiency and prey availability and size, so that the fish were eating the prey type most profitable in terms of energy gain. Persson (1987b) found that age 1+ perch (mean length 86 mm) had higher capture rates, higher net energy intake, and lower handling times when feeding on *Daphnia* than age 2+ perch (mean length 114 mm). Age 2+ perch had higher capture rates when feeding on *Sialis* (Megaloptera) and chironimids and higher net enery intake when feeding on *Sialis* that the younger perch. The shift in diet in late summer to zooplankton by both size classes of perch seems to be in response to decreasing abundance of benthic invertebrates and therefore increasing levels of competition for those invertebrates. Low availability of macroinvertebrates in the littoral zone was limiting the growth of pereh in Narrow Lake.

In Narrow Lake, the growth of y-o-y and older perch is less than in nearby lakes, indicating zooplankton as well as macroinvertebrates are insufficient to support normal growth. The macroinvertebrate feeding stage is commonly viewed as the bottleneck in the growth in individuals in stunted populations (Alm 1946, Keast 1977, Persson 1983a). Growth of y-o-y perch feeding on zooplankton in populations of stunted perch is often comparable to the growth of y-o-y in near by lakes, suggesting that an adequate supply of zooplankton is available (Keast 1977). However, slower growth than expected by older perch in the same lake where growth of the y-o-y was normal suggests that a bottleneck to growth occurs when the fish enter the next feeding stage (Keast 1977, Persson 1983a). Young-of-the-year perch in Narrow Lake show a decrease in growth rate when they move into the littoral zone (D. Abbey, pers. comm.) where older perch are feeding on zooplankton. This suggests that competition for zooplankton is occurring.

Some evidence exists in other lakes to indicated that young perch may be resource limited during the zooplankton feeding interval. In Lake Sövdeborg, Sweden, y-o-y (mean 3.5 g) in a stunted perch population fed on macroinvertebrates in August prior to 1980 when the roach population was reduced by 70% in number and 40% in biomass (Persson 1986). Then,

the y-o-y fed on zooplankton throughout the summer and the growth rates of age 1+ to 3+ perch increased. Persson (1986) suggested that previous to the roach removal zooplankton was limited by the roach and the y-o-y were forced to switch to macroinvertebrates at an early age. After roach removal, the older perch did not have to compete with the y-o-y perch for macroinvertebrates and therefore were released from the bottleneck which was restricting their growth. Persson (1987a) concluded that y-o-y perch are resource limited in the presence of roach and were forced to fed on copepods and macroinvertebrates instead of zooplankton. The older perch were food limited also because they were competing with the y-o-y for macroinvertebrates.

In Narrow Lake, perch may be resource limited both during the zooplankton and macroinvertebrate feeding interval. Food limitation across all sizes of fish will favor stunting. The decrease in the growth and condition of perch <4.0 g during July occurs near the shift in the diets from being dominated in weight and frequency by amphipods to being dominated by zooplankton.

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V. GENERAL CONCLUSION

This study provides the first detailed examination of a population of stunted yellow perch. The perch in Narrow Lake are the slowest growing perch yet reported in Canada. The stunted condition of the perch appears to be stable and is maintained by population characteristics such as high abundance, high reproductive potential, and the extremely slow growth rate. Since growth is slow, the age classes do not vary greatly in size, and the population has a small size class diversity. One major finding in this study was that the population was dominated by individuals <85 mm TL (excluding y-o-y), in contrast to other studies which found the dominant size class in populations of stunted perch to be larger. Their findings, though, are biased partially as a result of limited sampling techniques (eg. Rask 1983, Rask and Arvola 1985, Lappalainen *et al.* 1988).

The potential for competition would be greatest within the dominant size class in Narrow Lake. When invertebrate prey abundance is low relative to the number of perch, the growth of all individuals is decreased. In turn, the slow growth will increase the number of individuals in the dominant size class and a positive feedback system will operate to sustain the stunting. Persson (1983) predicted that a result of competition is the close packing of age and size classes and therefore a reduction in size class diversity. Low size class diversity was found in the population in Narrow Lake. Smaller perch have an advantage over larger individuals with respect to feeding on zooplankton, and therefore small perch may be favored when macroinvertebrates abundance is low (Persson 1987b). Since small individuals are able to tolerate lower resource levels, continued recruitment by the small young fish results in a population of small-bodied individuals (Mittelbach 1983). Small size and low age at maturity, characteristics of the perch in Narrow Lake, will therefore maintain the stunted population.

The second major finding in this study was that the growth and condition of age 1+ perch in Narrow Lake decreased in July. The decreases corresponded to a change in abundance of benthic invertebrates and the beginning of a shift in diet of the age 1+ perch from macroinvertebrates to being dominated by zooplankton. Feeding stages including these invertebrates can lead to competitive bottlenecks and reduced growth (Keast 1977, Gilliam

1980, Persson 1987a). A competitive bottleneck appears to be operating for age 1+ perch in Narrow Lake in July.

The intensity of the competition in Narrow Lake changed as summer progressed, since the condition and growth rate of the perch increased in August. High mortality of y-o-y perch after they move into the littoral zone would reduce the intensity of competition for zooplankton in August as compared to July when they first entered the zone. Thus, although more microinvertebrates were eaten by the age 1+ perch in August than July, their growth and condition was better. Weatherley (1972) suggested that competition between individuals is discontinuous and restricted to limited periods. Any environmental variation can influence competitive interactions so that competition is an intermittent process (Wiens 1977). In Narrow Lake, my data suggest that the age 1+ perch were food limited, more so in July than at other times during the summer.

The field experiment demonstrated that competition for macroinvertebrates was occurring within the dominant size class of perch. At high levels of intraspecific competition in the enclosures, growth rate, condition, and stomach fullness decreased and more microinvertebrates were eaten. These findings support the hypotheses proposed by Hanson and Leggett (1986). Fish at the highest levels of competition lost weight during the experiments, which indicated that foraging and maintenance energy demands were higher than net energy intake. The July experiment showed that the growth of perch at the lowest density was better than for perch of a similar size in the lake. This finding provided corroborating evidence that the age 1+ perch in the lake were competing for invertebrate food resources at that time of the summer.

Within enclosures at perch densities less than 7 g/m^2, no effect of perch density was observed on quantity or type of food consumed for each experiment conducted in July and August. However, growth varied inversely with perch density within each experiment. Although the perch in the enclosures at these densities were able to eat the same quantity and type of prey, the cost of feeding must be greater at the higher densities because growth was affected. In addition, the cost of feeding was greater in the August experiment when the perch

were feeding on a greater proportion of microinvertebrates than in July when microinvertebrates were less important in the diet. Perch had a negative growth rate which was inversely related to stocking density in August whereas the perch at the same densities had positive growth rates in the July experiment. Microinvertebrates can be an inferior food source for perch which have fed on larger prey items (Persson 1987b). At the highest densities, and the highest level of competition, the zooplankton was not a sufficient energy source for the perch to maintain a positive growth rate.

In conclusion, regardless of what factors initiated the stunting of the perch in Narrow Lake, the characteristics of the population maintain the stunting. Both the macroinvertebrate and zooplankton feeding stages appear to act as bottlenecks for the age 1+ perch, especially during July.

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Appendix 1 Table 1. Number of yellow perch caught by block seine in Narrow Lake as a function of sampling site and time of catch. Sampling times: morning - 09:00 to 10:30; afternoon = 11:00 to 16:00; evening = after 16:00.

Time period of sample	Sampling site	Number of perch in size class	
		<84 mm	≥ 85 mm
Morning	site 2	15	0
		53	12
	site 4	84	5
Afternoon	site 2	350	6
		103	72
		188	9
		235	9
		124	18
	site 3	108	8
		321	34
		114	11
		379	31
	site 4	325	32
		583	64
Evening	site 2	76	19
		68	19
	site 3	3	14
Morning	site 1	9	0
Afternoon		6	0

Appendix 1 Table 2. Effect of two weeks freezing on the weight of 24 yellow perch from Narrow Lake. Perch were marked individually, measured twice before freezing (blotted wet weight; g), frozen for two weeks, and remeasured. Paired t-tests were performed to assess the effect of freezing on perch weight and to assess the variation in remeasuring.

Before freezing				After freezing	
Weight measurement					
First a	Second b	Change a-b=c	Mean d=c/2	Weight e	Change f=d-e
5.59	5.62	0.03	5.61	5.56	0.05
3.45	3.45	0.00	3.45	3.50	0.05
3.41	3.34	0.07	3.38	3.31	0.06
3.12	3.12	0.00	3.12	3.08	0.04
3.07	3.04	0.03	3.06	3.03	0.03
2.90	2.85	0.05	2.88	2.87	0.00
2.76	2.76	0.00	2.76	2.72	0.04
2.54	2.52	0.02	2.53	2.44	0.09
2.36	2.33	0.03	2.35	2.33	0.02
2.02	1.99	0.03	2.01	1.96	0.04
1.96	1.95	0.01	1.96	1.93	0.03
1.64	1.64	0.00	1.64	1.62	0.02
1.48	1.49	0.01	1.49	1.44	0.05
1.47	1.47	0.00	1.47	1.47	0.00
1.43	1.41	0.02	1.42	1.42	0.00
1.43	1.40	0.03	1.42	1.40	0.02
1.46	1.40	0.06	1.43	1.40	0.03
1.38	1.38	0.00	1.38	1.40	0.02
1.20	1.17	0.03	1.19	1.16	0.03
2.90			2.90	2.91	0.01
2.89			2.89	2.90	0.01
2.63			2.63	2.61	0.02
3.46			3.46	3.43	0.03
4.12			4.12	4.03	0.09

Paired t-tests

Ho: c=0	Ho: a=b
mean±SD: -0.02±0.03	mean±SD: -0.02±0.02
n=24	n=19
t-stat=-3.72	t-stat=-2.80
t_{23}=2.07	t_{18}=2.10
P>0.001 reject Ho	P>0.01 reject Ho

Appendix 1 Table 3. Effect of two weeks freezing on total length measurements of yellow perch from Narrow Lake. Perch (n=20) were individually marked, measured, frozen for two weeks and measured again. A paired t-test was performed to assess the difference in total length before and after freezing.

Total length (mm)		Difference between comparisons
before freezing a	after freezing b	c=b-a
84.8	83.7	-1.1
75.2	75.0	-0.2
75.1	74.0	-1.1
75.2	73.6	-1.6
70.2	69.6	-0.6
70.7	69.5	-1.2
70.9	69.0	-1.9
70.5	68.6	-1.9
68.7	68.3	-0.4
69.1	68.0	-1.1
67.1	67.0	-0.1
65.3	64.0	-1.3
62.3	62.2	-0.1
57.4	56.1	-1.3
57.1	55.7	-1.4
56.5	55.5	-1.0
55.9	54.5	-1.4
54.5	54.0	-0.5
55.5	54.0	-1.5
53.5	52.8	-0.7

Paired t-test
Ho: a=b; H_1: a≠b
mean±SD
-1.0±0.6
n=20
computed t-stat = -8.06
P>0.001 reject Ho

Appendix 1 Table 4. Catch of yellow perch and northern pike in seine hauls done at Narrow Lake, Alberta, on August 24-26, 1986, June 2,4, 1987, Aug. 24, 26, 1987 and Aug. 23, 1988. All seine hauls were done between 10:00 and 17:00. The seine enclosed a 500-m^2 area.

Date	Perch Weight (g/haul)	Perch (No./ haul)	Pike Weight (g/haul)	Pike (No./ haul)
Aug. 86	500.8	112	802.1	8
	534.9	125	22.3	9
	571.1	142	371.1	4
	1253.7	355	77.5	7
	660.4	197	22.5	3
	2155.5	647	1731.2	4
	1297.5	410	281.9	5
	781.7	244	51.8	3
	453.0	116	358.3	3
	976.3	356	18.1	1
	1180.6	357	122.8	2
June 1987	301.9	162	13.7	1
	797.0	116	0	0
	269.5	195	0	0
	1222.2	868	0	0
	92.6	83	1362.0	2
	2473.1	357	720.9	2
	9.4	2	348.1	1
	5.8	4	0	0
	11.2	7	0	0
	6.0	4	0	0
	5.4	5	0	0
Aug. 1987	246.4	59	18.7	2
	130.5	21	17.5	3
	79.4	29	4.0	1
	164.8	60	2182.0	4
	456.5	97	649.8	3
	138.5	28	0	0
	376.4	118	10.7	1
	333.0	80	908.6	3
	353.9	42	0	0
	118.9	30	78.5	2
	166.2	44	295.6	5
	29.3	7	8.0	1
	39.0	8	0	0
Aug. 1988	847.3	175		
	166.3	22		
	931.6	219		
	252.1	65		
	54.5	6		
	1431.7	284		
	99.5	31		

Appendix 1 Table 5. Growth rates of age 1+ yellow perch from Narrow Lake during May-August, 1986-1988.

Date	Weight (g)	Month Interval	No. of days	Growth rate (g/day)	% of initial /day
1986					
May 18	1.15				
June 25	1.98	May-June	51	0.020	1.8
July 8	2.19				
July 22	2.23	July	28	0.001	0.1
August 5	2.22				
August 19	2.49				
August 27	2.71	August	22	0.022	1.9
1987					
May 7	0.91				
May 18	0.97	May	25	0.005	0.5
June 1	1.03				
June 5	1.21				
July 1	1.59	June	30	0.019	2.0
July 8	1.86				
July 27	2.04	July	26	0.010	1.1
August 3	2.13				
August 24	2.48	August	21	0.017	1.8
1988					
May 18	0.97				
June 2	1.03	June	43	0.022	2.5
June 30	1.21				
July 13	1.59				
July 25	2.04	July	26	0.014	1.6
August 8	2.13				
August 23	2.48	August	15	0.032	3.6

Appendix 2 Table 1. Stocking schedule of perch in two enclosure experiments conducted in 1986 testing for evidence of intraspecific competition. Perch used in the experiments were between 1.5 and 3.1 g (average weight ± SD = 2.34 ± 0.36 g). Perch in the enclosures stocked at 5 g/m² were lost in both experiments and therefore the lowest density enclosure was omitted in both experiments.

Experiment	Perch Weight ± SD (g)	Density Treatment (g/m²)	No. Stocked/ enclosure
First	Stocking date July 15		
	2.19 ± 0.21	8.4	45
	2.08 ± 0.26	14.9	66
Second	Stocking date Aug. 18		
	2.55 ± 0.30	9.9	36
	2.57 ± 0.30	14.6	54

Appendix 2 Table 2. Stocking schedule of perch in three enclosure experiments conducted in 1987 to test for evidence of intraspecific competition. Perch used in the experiments were between 1.5 and 3.1 g. The duration of each experiment was 21 days. One enclosure stocked at medium perch density in the July experiment was omitted because one pike (12 g, with one marked perch in its stomach) was caught at the end of the experiment. Unmarked perch were caught in five enclosures of the August experiment, and three enclosures were omitted from analyses since there was more than a two-fold difference between the number of perch stocked and the number of perch recovered.

Experiment	Treatment	Density Treatment (g/m^3)	Perch Weight ± SD (g)	Number stocked/ enclosure
		Stocking date		
June		June 10		
	Low	2.1	1.93±0.27	10
		2.3	1.93±0.36	11
	Medium	4.1	1.87±0.35	18
		4.1	1.77±0.25	18
	High	6.1	1.92±0.50	29
		6.0	2.01±0.45	28
July		July 1		
	Low	3.0	2.21±0.31	14
		3.2	1.92±0.32	13
	Medium	5.4	1.98±0.31	26
	High	7.0	1.80±0.29	32
		7.1	2.15±0.47	29
August		August 3		
	Low	3.2	2.06±0.28	14
	Medium	5.2	2.24±0.45	21
	High	7.1	2.38±0.28	30

Appendix 3 Table 1. Stomach fullness (mg food/g fish) of perch caught during two 24-h feeding studies in 1986. Data presented are the original means±SE and the transformed means±SE calculated using the Robust General Linear Model (Kapenga *et al.* 1988).

Time	Perch No.	Original mean±SE	transformed mean±SE
July 8-9			
12:00	11	1.29±0.55	0.03±0.65
15:00	14	1.28±0.68	0.00±0.58
18:00	15	0.30±0.23	0.00±0..56
21:00	14	3.16±1.65	0.15±0.58
24:00	13	5.36±0.97	4.24±0.61
03:00	14	4.98±1.47	3.18±0.58
06:00	12	11.04±2.54	7.90±0.63
09:00	13	3.37±0.72	2.58±0..60
August 3-4			
12:00	14	10.76±3.07	6.26±1.27
18:00	15	2.49±0.97	1.19±1.22
21:00	12	12.50±3.88	7.15±1.38
24:00	14	0.36±0.16	0.09±1.27
06:30	20	15.60±2.36	13.49±1.04
09:00	17	8.16±1.10	7.22±1.14
12:00	15	8.15±2.28	6.48±1.22

Appendix 3 Table 2. Proportion of microinvertebrates in the diet (mg microinvertebrates/mg total stomach contents) of perch in enclosures at various densities and in Narrow Lake in experiments testing for evidence of intraspecific competition. Data presented are the original means±SE and the transformed means±SE calculated using the Robust General Linear Model (Kapenga *et al.* 1988). Data of perch from the lake are indicated by asterisks.

Experiment	Density g/m²	Perch No.	Original mean±SE	transformed mean±SE
1986				
First	7.4	21	0.29±0.87	0.18±0.04
	10.4	24	0.74±0.08	0.91±0.04
	2.6*	15	0.80±0.10	1.00±0.05
Second	6.8	20	0.63±0.09	0.82±0.09
	10.3	19	0.78±0.07	0.91±0.10
1987				
June†	1.8	16	0.04±0.04	
	3.5	19	0.02±0.01	
	5.0	20	0.02±0.01	
	1.1*	11	0.42±0.14	
July	3.6	20	0.26±0.09	0.27±0.11
	6.1	11	0.28±0.11	0.27±0.14
	7.0	25	0.57±0.09	0.61±0.11
	1.1*	20	0.37±0.09	0.36±0.11
August	3.8	13	0.52±0.14	0.57±0.13
	4.1	13	0.71±0.11	0.78±0.13
	6.6	9	0.77±0.14	0.86±0.15
	1.4*	15	0.86±0.05	0.88±0.12

†As a result of rounding error, the RGLM package was unable to do an ANOVA on the data from the June experiment (T. Taerum, pers. comm.).